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REVISION OF *DICHANTHELIUM* SECT. *LANUGINOSA* (POACEAE)

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ABSTRACT

Debate and confusion have persisted regarding the morphological ranges and limits of those taxa found within *Dichanthelium* sect. *Lanuginosa*. Phenetic analysis, principal components analysis, and pair-wise t-tests of character states were conducted with 285 specimens using 32 morphological characters. An additional examination of 2780 herbarium specimens, including all relevant type material, resulted in the recognition of 16 species and one subspecies. Many of the entities currently subsumed within the *D. acuminatum* and *D. ovale* complexes are here interpreted to represent distinct species in terms of morphology. Many of these taxa were secondarily found to exhibit geographical and ecological distinctions, which are also discussed. All 160 names associated with the section are reviewed and an accurate nomenclature is applied to the group. *Dichanthelium lanuginosum* is reinstated as distinct from *D. acuminatum* and two new nomenclatural combinations are proposed: **Dichanthelium thermale** (Bol.) J. Thomas, **comb. nov.** and **Dichanthelium thermale** subsp. **sericeum** (Schmoll) J. Thomas, **comb. nov.**

Dichanthelium is one of the largest genera of New World grasses. Because of its diversity and wide distribution, a taxonomic understanding of the genus is vital to floristic treatments, monitoring projects, restoration efforts, and other areas of conservation and taxonomic concern. Hitchcock and Chase (1910) published *Dichanthelium* as a subgenus of *Panicum* to accommodate those taxa that produce terminal and axillary inflorescences (floral dimorphism), possess winter rosettes in addition to cauline leaves (foliar dimorphism), and rounded rather than pointed spikelets. This is in contrast to members of subg. *Panicum*, which only produce terminal inflorescences, lack winter rosettes, and generally have pointed spikelets. In addition to these differences, more contemporary studies have demonstrated further distinctions between *Dichanthelium* and *Panicum*. Brown (1948), Smith and Brown (1973), and Brown and Smith (1975) demonstrated that members of subg. *Dichanthelium* utilize C3 photosynthetic pathways as opposed to members of subg. *Panicum*, which are primarily C4 grasses. Boyle (1945) reported that subg. *Dichanthelium* has an extremely low incidence of polyploidy (only 3 out of approximately 100 species) whereas 70–80% of subg. *Panicum* species are polyploid. Brown et al. (1957) noted that subg. *Dichanthelium* has two layers of tunica cells in the shoot apices whereas subg. *Panicum* has a single layer.

Given the extent of such differences, Gould (1974) elevated subg. *Dichanthelium* to the rank of genus. However, some taxonomists have been hesitant to accept this status change, noting an abundance of tropical species that appear to be intermediate between the two genera (Lelong 1986; Webster 1988; Crins 1991; Gleason & Cronquist 1991; Yatskievych 1999). The argument against elevation of *Dichanthelium* to generic rank was further supported by Morrone and Zuloaga (1991) and Zuloaga et al. (1993a, b), who tested the evidence defending *Dichanthelium* as a distinct genus. Their results indicate intermediates and exceptions regarding foliar and floral dimorphism, ploidy level, and C3 versus C4 photosynthesis, especially in Central and South American species. More recent evidence has come from research involving the molecular phylogeny of Panicoideae (Giussani et al. 2001; Aliscioni et al. 2003; Morrone et al. 2008). These studies demonstrate that *Panicum s.l.* is polyphyletic unless *Dichanthelium*, among others, is treated as a separate genus. Additionally, many of the presumed intermediate taxa (most notably *Panicum* sect. *Cordovensia*) that were used to maintain *Dichanthelium* as a subgenus of *Panicum* have been shown to represent distinct lineages (Aliscioni et al. 2003; Morrone et al. 2008). Though debate may still be pertinent, the current tide of evidence seems to best support *Dichanthelium* as a distinct genus. The development of an over-

wintering rosette in this group of grasses may have led to the diversification of *Dichanthelium* into temperate North America (Morrone 1991; Zuloaga et al. 1993b) and this foliar dimorphism does offer a reasonable synapomorphy for the genus.

Dichanthelium includes 72–109 species (Gould & Clark 1978; Freckmann & Lelong 2003; Hitchcock & Chase 1910). Most are native to North America (Freckmann & Lelong 2003) but they are also found in South America and the Antilles. Members of the genus are perennials that have erect to decumbent stems that range from 5–150 cm long, vary greatly in degrees of pubescence, and often have short, wide leaves relative to other grasses. *Dichanthelium* species experience two flowering periods per growing season (Freckmann & Lelong 2003): a terminal paniculate inflorescence in spring followed by mid-summer inflorescences on axillary branches that bloom through autumn. The spikelets of the vernal inflorescences are reportedly chasmogamous, while those of the autumnal inflorescences are occasionally cleistogamous (Zuloaga et al. 1993b). The spikelets of *Dichanthelium* range from 0.8–5.2 mm in length and typically have morphologically dissimilar glumes, one sterile lemma, and a single fertile floret (Freckmann & Lelong 2003).

In 1910, Hitchcock and Chase arranged the taxa of what they treated as subg. *Dichanthelium* into 17 informal groups based on morphological characters. Many authors since have incorrectly used these names as subgenera, sections, or sub-sections, but only more recently have any groups been validly published as sections within *Dichanthelium* (Freckmann & Lelong 2002). In so doing, Freckmann and Lelong (2002) reduced the 17 informal groups of Hitchcock and Chase (1910, 1951) to 13 sections (*Angustifolia*, *Clandestina*, *Dichanthelium*, *Ensifolia*, *Lancearia*, *Lanuginosa*, *Linearifolia*, *Macrocarpa*, *Nudicaulia*, *Pedicellata*, *Oligosantha*, *Sphaerocarpa*, and *Strigosa*). The informal groups *Lanuginosa*, *Spreta*, and *Columbiana* of Hitchcock and Chase (1910, 1951) (Table 1) were all included in sect. *Lanuginosa* by the treatment of Freckmann and Lelong (2002). As defined by Freckmann and Lelong (2002), sect. *Lanuginosa* differs from other sections by the following combination of characters: vernal leaves distributed along the stem (not basally disposed), ciliate ligules ranging from 0.2 to 4.7 mm long, pubescent spikelets that are elliptical in outline, and primary glumes that are less than half the length of the spikelet.

According to Freckmann and Lelong (2003) sect. *Lanuginosa* comprises 3 North American species and 12 subspecies. This is a significant reduction in the number of taxa from the treatment of Hitchcock and Chase (1910, 1951), who recognized 33 species and 2 varieties (Table 1). Without discussion, Gould and Clark (1978) recognized 3 species and 9 varieties within what is now sect. *Lanuginosa* (Table 1). Many regional treatments (Braun 1967; Freckmann 1981; Gleason & Cronquist 1991; Hansen & Wunderlin 1988; Lelong 1984; Mohlenbrock 1986; Radford et al. 1968; Steyermark 1963; Strausbaugh & Core 1978; Swink & Wilhelm 1994; Voss 1972; Weishaupt 1968) appear to reflect Fernald's (1934, 1950) conservative treatments of those taxa occurring in northeastern North America. However, confusion and frustration still persist regarding the regional application of delineated taxa within the section.

It has been noted (Freckmann 1981; Gould & Clark 1978; Hansen & Wunderlin 1988; Swink & Wilhelm 1994; Voss & Reznicek 2012; Yatskievych 1999) that in order to understand the species complexes within *Dichanthelium*, detailed morphological and population-level studies will be necessary. Though Shinners (1944) conducted an informal investigation into the "empirically existing discontinuities" of a few taxa within sect. *Lanuginosa*, a thorough analysis of the morphological diversity has never been published. Due to the enthusiasm with which late 19th Century botanists described the variation in sect. *Lanuginosa*, an abundance of subsequent treatments attempting to render regional clarity and the subsumption of many regional taxa by modern treatments, we are left with a convoluted history of splitting and lumping of sections, species, subspecies, and varieties, often with little or no justification. The taxonomic confusion of the section appears to rests on the widely varying emphasis of ligule, pubescence, and spikelet characters. The primary goals of the present study are to (1) statistically investigate the morphological variation

within sect. *Lanuginosa* in order to elucidate the natural boundaries of the taxa within, (2) review all available literature and type material in order to provide and apply an accurate nomenclature, (3) test the results of the data analysis against specimens from throughout the geographic range of the section, and (4) investigate and report the ecological and geographical context of each taxon.

Hitchcock and Chase, 1910	**Gould and Clark, 1978**	**Freckmann and Lelong, 2003**
Group *Columbiana*	No subgeneric rank given	Section *Lanuginosa*
Panicum addisonii	*D. sabulorum* var. *patulum*	*Dichanthelium acuminatum*
P. columbianum	var. *thinium*	subsp. *acuminatum*
var. *columbianum*	*D. ovale* var. *ovale*	subsp. *columbianum*
var. *thinium*	var. *addisonii*	subsp. *fasciculatum*
P. commonsianum	*D. acuminatum* var. *acuminatum*	subsp. *implicatum*
P. malacon	var. *densiflorum*	subsp. *leucothrix*
P. oricola	var. *implicatum*	subsp. *lindheimeri*
P. tsugetorum	var. *lindheimeri*	subsp. *longiligulatum*
P. wilmingtonense	var. *longiligulatum*	subsp. *sericeum*
	var. *thurowii*	subsp. *spretum*
Group *Lanuginosa*	var. *villosum*	subsp. *thermale*
P. acuminatum	var. *wrightianum*	*D. ovale* subsp. *ovale*
P. albemarlense		subsp. *praecocius*
P. auburne		subsp. *pseudopubescens*
P. huachucae var. *huachucae*		subsp. *villosissimum*
var. *silvicola*		*D. wrightianum*
P. implicatum		
P. languidum		
P. lanuginosum		
P. meridionale		
P. occidentale		
P. olivaceum		
P. ovale		
P. pacificum		
P. praecocius		
P. pseudopubescens		
P. scoparioides		
P. shastense		
P. subvillosum		
P. tennesseense		
P. thermale		
P. thurowii		
P. villosissimum		
Group *Spreta*		
P. leucothrix		
P. lindheimeri		
P. longiligulatum		
P. spretum		
P. wrightianum		

Table 1. Summary of past taxonomic treatments for all taxa involved in sect. *Lanuginosa*.

METHODS

A total of 2780 specimens, including type specimens, from throughout the geographical range of sect. *Lanuginosa* was examined from several herbaria (F, GH, MIN, MO, MU, NCU, NY, URV, US, WIS, WS). From these, a subset of specimens representing the morphological and geographical range of sect. *Lanuginosa* was compiled. Specimens that lacked ample fertile or vegetative material for sampling were not included in the data set. These specimens were sampled for 104 vegetative characters and 12 floral characters. These data were then analyzed via histograms (Appendix B) and an analysis of character means in order to eliminate any characters that were invariant or unimodal throughout the data set. This was largely done to reduce the number of measured characters and thereby increase the number of specimens that could be sampled during the time frame of the study. Using the remaining 32 characters (Table 2), 285 specimens were sampled. All type specimens that possessed sufficient characters were included in the sampling. In order to further maximize efficiency and focus on the confusing morphological complexes in the section, more specimens were sampled from the notoriously problematic "morpho-groups" than from the more obviously distinct ones. For example, all previous treatments have maintained *Dichanthelium wrightianum* as a morphologically distinct taxon, therefore few specimens, only later associated with this name, were sampled for what could be interpreted as this morphology.

The data were entered into Microsoft Excel and imported into NT-SYS-pc 2.1 (Rohlf 2002) for analysis. In NT-SYS, the data were standardized, a similarity matrix was created, distance coefficients were computed and a phenogram was constructed by the sequential, agglomerative, hierarchical, and nested clustering method (SAHN) using the unweighted pair group method with arithmetic mean (UPGMA). This analysis resulted in a phenogram with two distinct clusters. The two clusters are here referred to as the Long Ligule Group and the Short Ligule Group. In order to more thoroughly and adequately investigate the significance of the morphological variation in the analysis as well as elucidate the morphological characters of taxonomic importance, the data were divided into these two groups and analyzed independently for the remainder of the analysis. It is important to note that this investigation is in no way an attempt to portray the evolutionary relationships within sect. *Lanuginosa*, nor is this analysis in accordance with the practices of numerical taxonomy. Rather, the main objective of this portion of the analysis is to remove as many constant, invariant, and unimodal variables as possible in order to empirically explain the different morphologies within the section and later test the strength of these differences via principal components analysis and other statistical methodologies outlined below. Splitting the data into two sets, a step justified by the SAHN clustering analysis, is one way to accomplish this.

Once the data were split into the Long Ligule Group and the Short Ligule Group, based primarily on the influence of ligule length in the SAHN cluster analysis, invariant characters were eliminated from each group, leaving 24 characters (Table 2) for the 142 specimens within the Long Ligule group and 12 characters (Table 2) for the 143 specimens within the Short Ligule group. Each of the two independent data sets was then reanalyzed by the SAHN clustering methodology above as well as by principal components analysis (PCA). All data in the PCA were standardized so that each character had an equal contribution to the variance in the analysis. The clusters of specimens generated by the SAHN cluster analysis and PCA were evaluated for similarity and consistency. Each of the resultant clusters was then analyzed by pair-wise comparisons, using two sample T-tests, in order to investigate the significance of the differences between clusters for each character. An additional PCA was conducted in order to further investigate the morphological variance of two slightly overlapping clusters in the Long Ligule Group — namely, those of *D. lanuginosum* and *D. implicatum*.

	Character	Abbreviation	Character State
1.	ligule pubescence maximum length	LigLen*‡	(mm)
2.	ligule trichome uniformity	LigTriUni*	0=no; 1=yes
3.	mid-stem sheath pubescence maximum length	MidShePubMax*	(mm)
4.	mid-stem sheath glabrous to glabrate	MidSheGla*	0=no; 1=yes
5.	mid-stem leaf adaxial pubescence maximum length	AdaLeaPubMax*	(mm)
6.	adaxial surface of mid-stem leaf glabrous to glabrate	AdaSurMidLeaGla*	0=no; 1=yes
7.	terminal sheath pubescence maximum length	TerShePubMax*	(mm)
8.	terminal sheath glabrous to glabrate	TerSheGla*	0=no; 1=yes
9.	terminal leaf abaxial pubescence minimum length	TerLeaAbaPubMin*	(mm)
10.	terminal leaf abaxial pubescence maximum length	TerLeaAbaPubMax*	(mm)
11.	spikelet length	SpiLen*‡	(mm)
12.	spikelet width	SpiWid*	(mm)
13.	first glume length	PriGluLen*‡	(mm)
14.	longest leaf length	LonLeaLen*	(mm)
15.	longest leaf width	LonLeaWid*‡	(mm)
16.	number of nodes in inflorescence	NumInfNod*	number
17.	inflorescence axis with puberulent pubescence	PubPubInf*	0=no; 1=yes
18.	peduncle glabrous to glabrate	PedGla*	0=no; 1=yes
19.	peduncle pubescence double invested	PedPubDou*	(mm)
20.	abaxial leaf surfaces with puberulent pubescence	AbaLeaSurPub*	0=no; 1=yes
21.	inflorescence < a third as long as wide	InfNar*	0=no; 1=yes
22.	fertile floret pointed	FerFloPoi*	0=no; 1=yes
23.	inflorescende w/ double vestiture	InfDouVes*	0=no; 1=yes
24.	spikelet pointed at apex	SpiPoi*	0=no; 1=yes
25.	double ligule conspicuous	DouLigCon‡	0=no; 1=yes
26.	double vestiture on culm	DouVes‡	0=no; 1=yes
27.	number of trichomes across mid-stem adaxial leaf surface	NumTriAdaLeaSur‡	number
28.	mid-stem leaf glabrous along middle of adaxial surface	MidLeaGlaAda‡	0=no; 1=yes
29.	terminal leaf glabrous along middle of adaxial surface	TerLeaGlaAda‡	0=no; 1=yes
30.	mid-stem sheath indument length	MidSheIndLen‡	(mm)
31.	sheath pubescence orientation	ShePubOri‡	scale; 0=appressed; 1=erect
32.	mid-stem leaf marginal cilia >30	Cilia>30‡	0=no; 1=yes

Table 2. Morphological characters used in the final phenetic analysis and principal components analysis. "*" indicates characters pertaining to the Long Ligule Group. "‡" indicates characters pertaining to the Short Ligule Group.

Based on the results of these analyses, preliminary groups and their defining morphological limits were determined. The range of character variability found in the data was then analyzed for consistency by testing the results against an additional 458 herbarium specimens from 33 states, 7 Canadian provinces, 4 Central American countries, and 3 Caribbean islands. A review of the literature and type specimens involved in sect. *Lanuginosa* was conducted in order to determine the appropriate application of nomenclature within the clusters generated in the data analysis. Once an accurate nomenclature was determined, a key was constructed from the data collected in the analysis and all 2780 specimens from the original compilation were examined, sorted, and annotated. Throughout the annotation process, detailed notes regarding the regional variation of each taxon and trait were taken. Distribution maps were compiled from the information provided on the herbarium labels of each specimen. Habitat information for each taxon was determined from the label information, previous treatments (where applicable), and from the author's 17 years of extensive field experience with the group.

RESULTS

Of the 116 morphological characters sampled using histogram and mean analysis, 32 proved informative. The SAHN cluster analysis of all 285 specimens for all 32 characters resulted in an obvious split of the data set into two major groups (Figure 1), here referred to as the Long Ligule Group and the Short Ligule Group. A review of all the characters in the analysis revealed that the length and distribution of ligule hairs were largely responsible for the division of the specimens into these two groups (Figure 2). The Long Ligule Group consistently possesses a uniformly long ligule pubescence that is indistinguishable from the pseudoligule, whenever present, and is always 1.7 mm long or longer. The Short Ligule Group primarily possesses a short ligule that is often, but not always, subtended by a longer pseudoligule. When the pseudoligule is short or intermeshed with the ligule, the ligule is often difficult to discern. In such cases, teasing the ligule with a probe revealed that the first row of ligule hairs was always 1.5 mm long or shorter. Given the strength of the split, its alignment with past treatments in which ligule length has always been a primary character, and in order to more precisely investigate the statistical variation in morphology within the section, each of these two groups were analyzed independently for the remainder of the study. Twenty of the 32 sampled characters were unique to the Long Ligule Group, 8 were unique to the Short Ligule Group and 4 were common to both groups (Table 2).

The independent SAHN cluster analyses of both the Long Ligule Group (Figure 3) and the Short Ligule Group (Figure 4) resulted in several clusters each. However, the degree to which these clusters represented discrete morpho-taxa was not apparent. A comparison of these results with those of the clusters derived from the PCA of each group (Figures 5 and 6), in conjunction with where the type specimens sorted within the clusters were ultimately used to elucidate the morpho-taxa represented in the data. Based on these results, the Long Ligule Group consisted of ten clusters and the Short Ligule Group consisted of seven clusters.

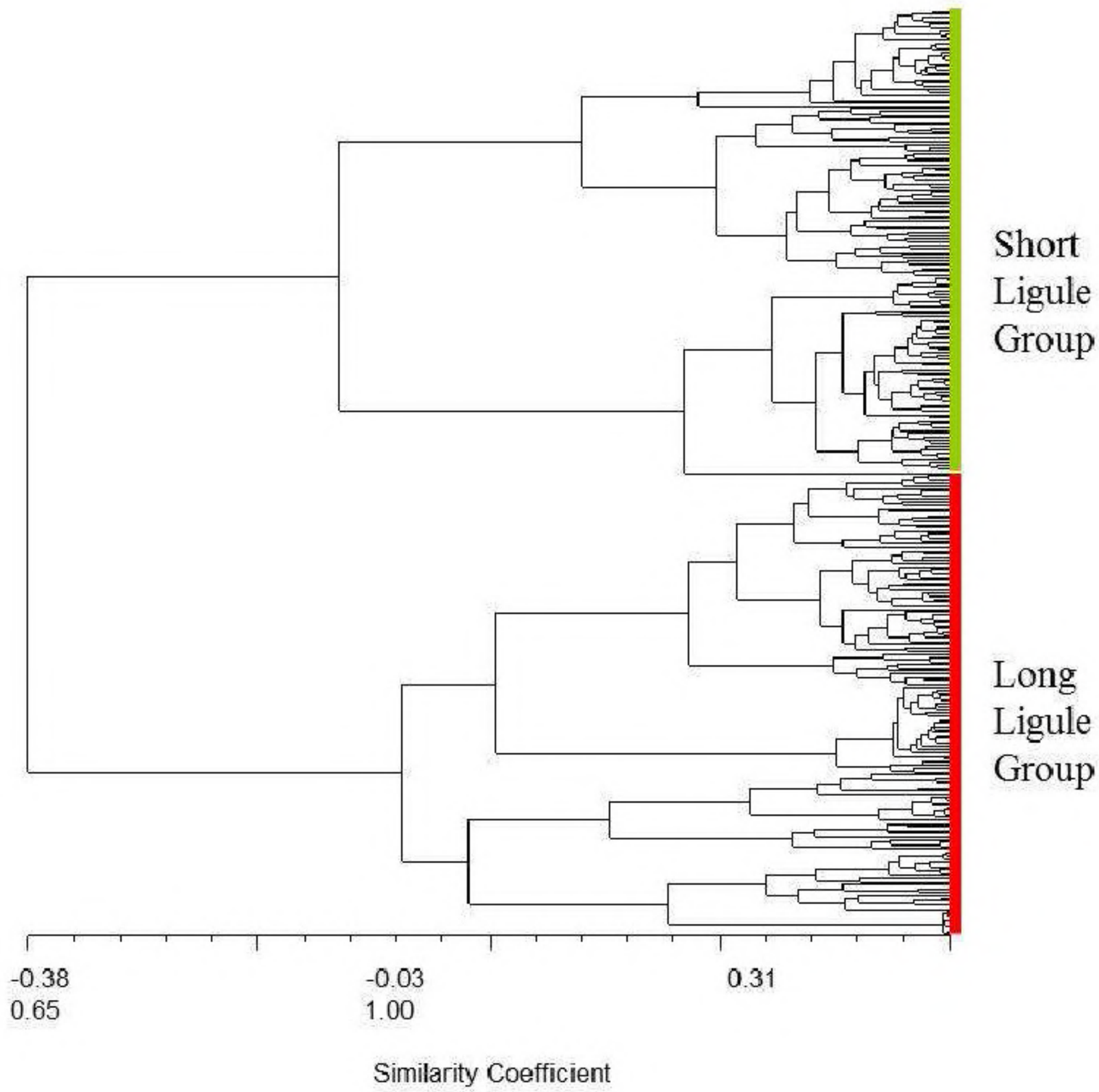


Figure 1. Phenogram for all 285 OTUs using 32 morphological characters. Cophenetic correlation coefficient (r) = 0.85.

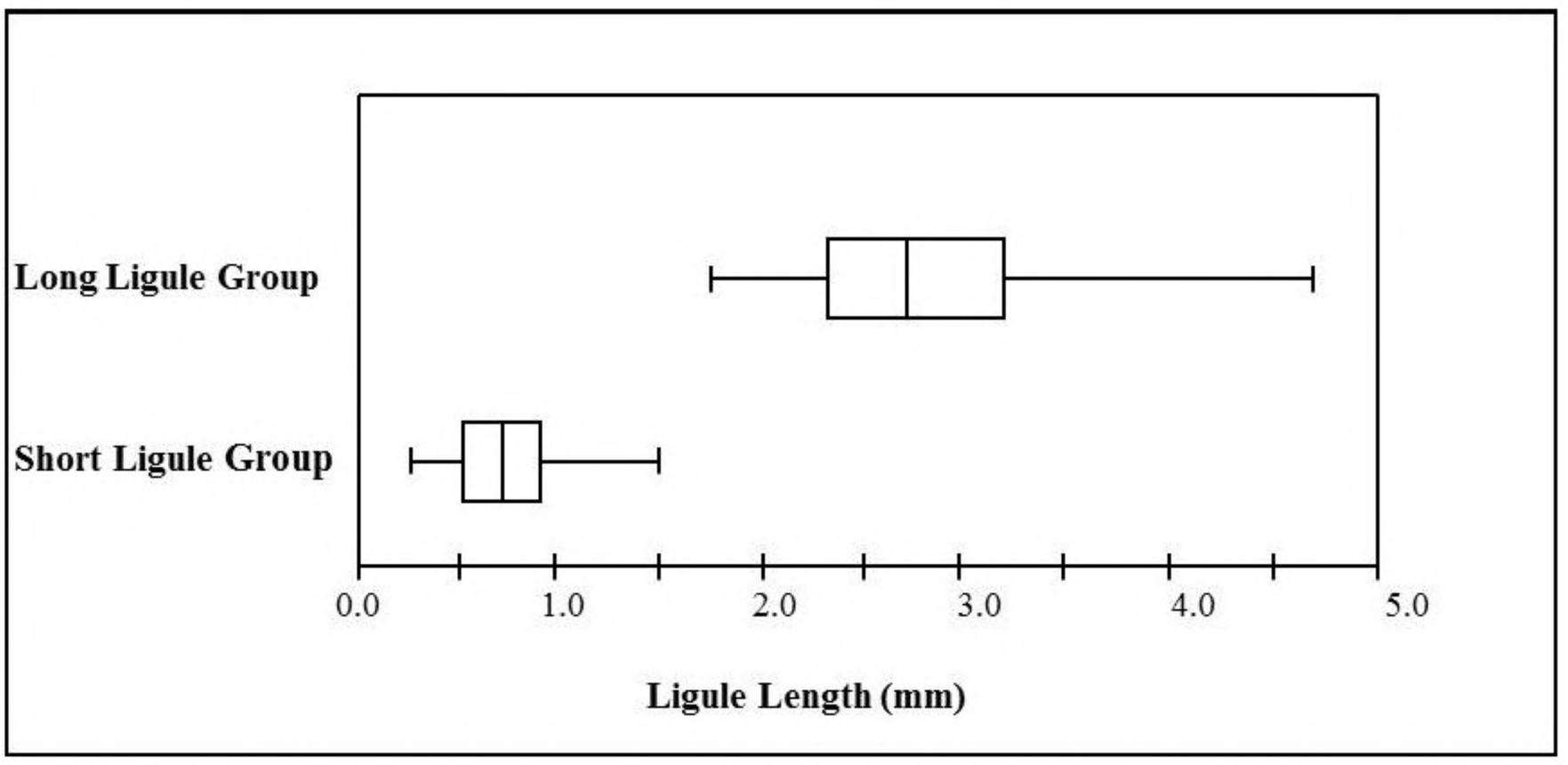


Figure 2. Box plot showing the lack of overlap in ligule length between the OTUs of the Long Ligule and Short Ligule groups.

In order to further investigate the strength of the clusters derived from the SAHN cluster analysis and PCA and to thereby assist in the assignment taxonomic ranks, pair-wise comparisons of each cluster for each character using two sample t-tests were conducted. The Long Ligule Group showed a significant difference of $P \leq 0.05$ for no less than nine and as many as 22 of the 24 characters sampled (Table 3). A significant difference of $P \leq 0.005$ was found for no less than four and as many as 20 of the characters (Table 3). For the Short Ligule Group, the two sample t-tests showed a significant difference of $P \leq 0.05$ for no less than four and as many as 11 of the 12 characters (Table 4). A significant difference of $P \leq 0.005$ was found for no less than three and as many as 11 characters (Table 4).

Within the Long Ligule Group, the first three principal component axes of the PCA accounted for 72 percent of the variation (Table 5). Nine clusters were separated by the first two principal component axes (Figure 5). Characters involving the length and density of pubescence along leaves and sheaths, as well as spikelet characters, contributed the most variation along the first principal component (PC1). Leaf length and characters involving the pubescence of the inflorescence contributed most to the variation along the second principle component (PC2).

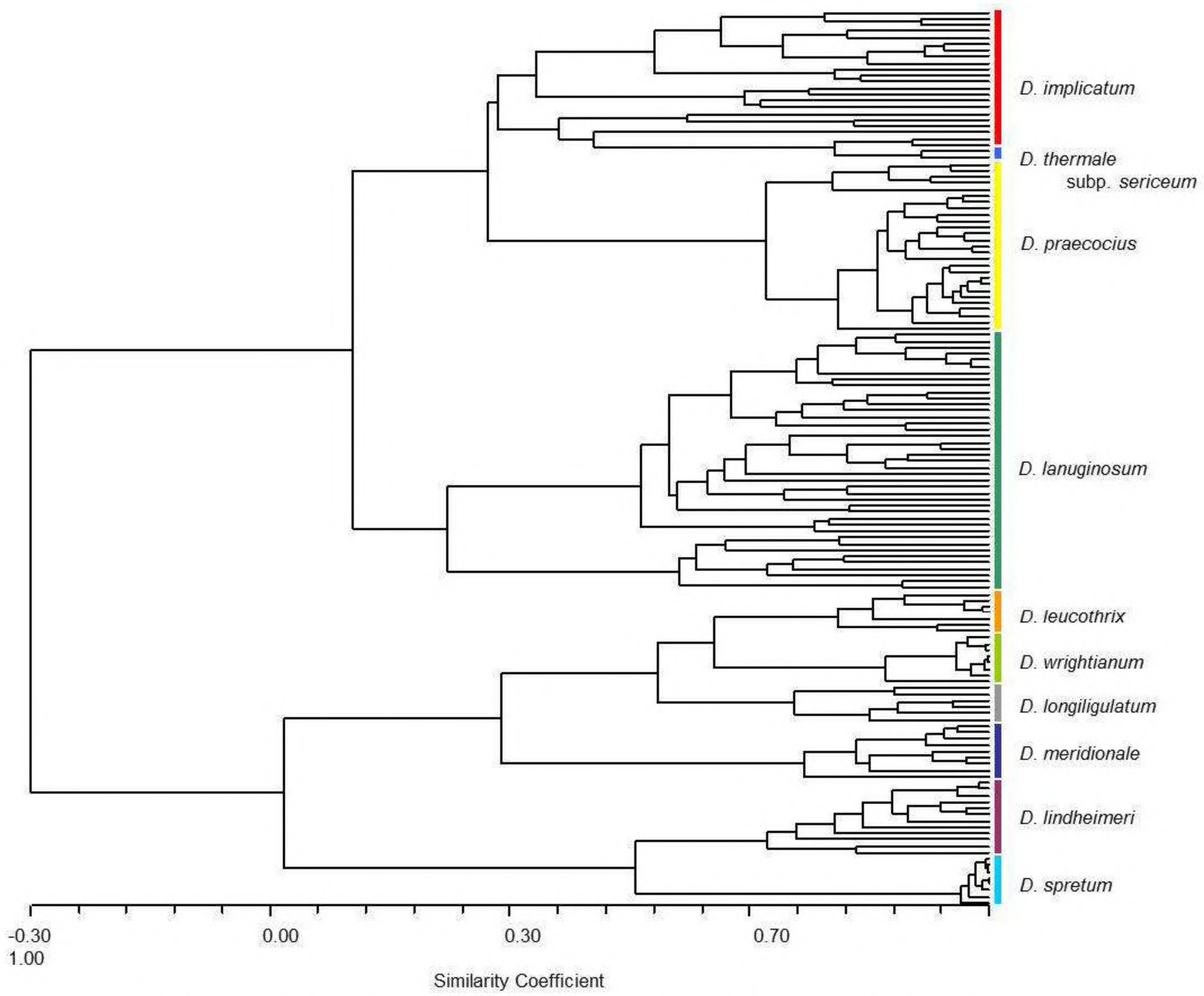


Figure 3. Phenogram of the Long Ligule Group based on 142 OTUs and 24 morphological characters. Cophenetic correlation coefficient (r) = 0.91.

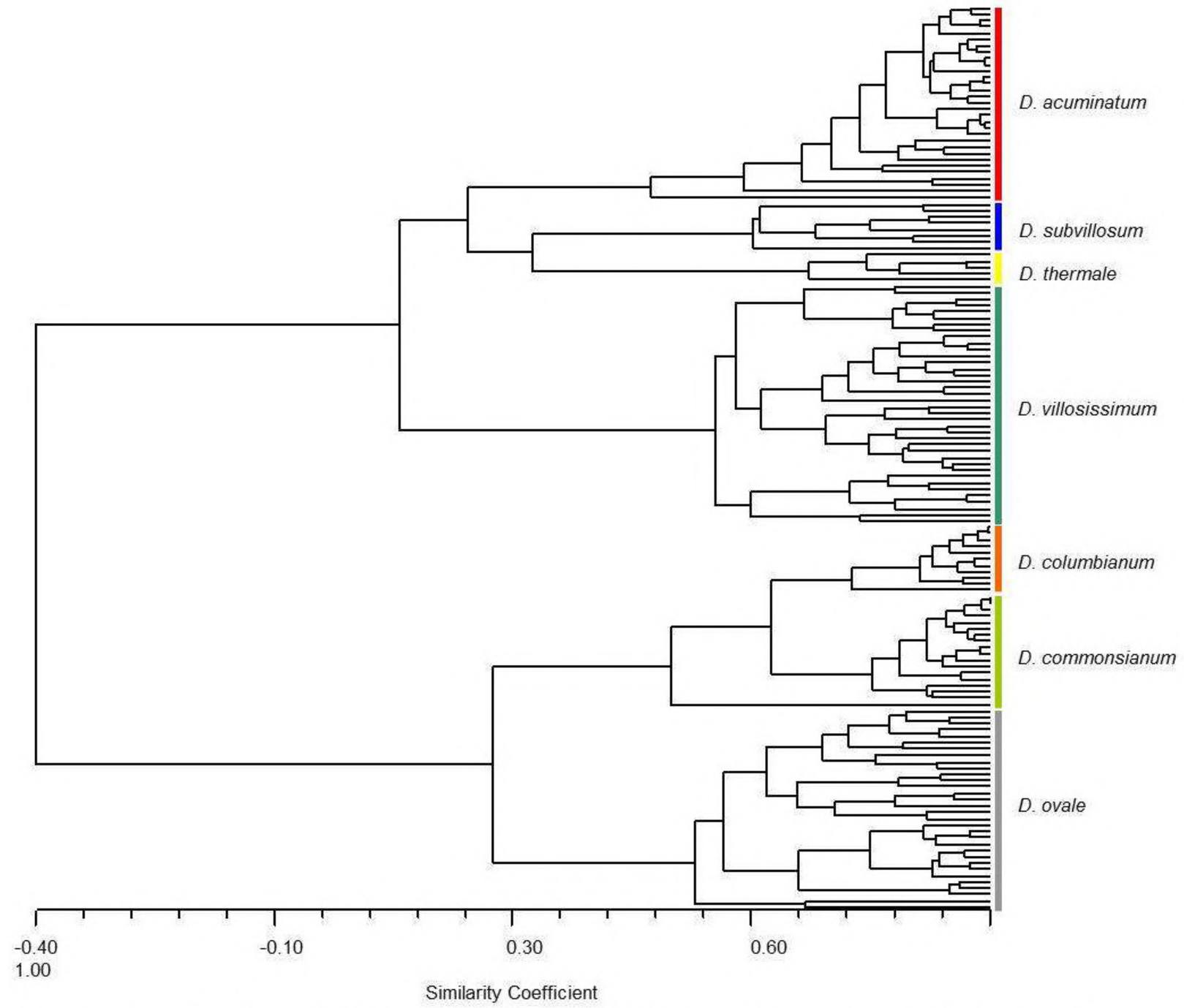


Figure 4. Phenogram of the Short Ligule Group based on 143 OTUs and 12 morphological characters. Cophenetic correlation coefficient (r) = 0.90.

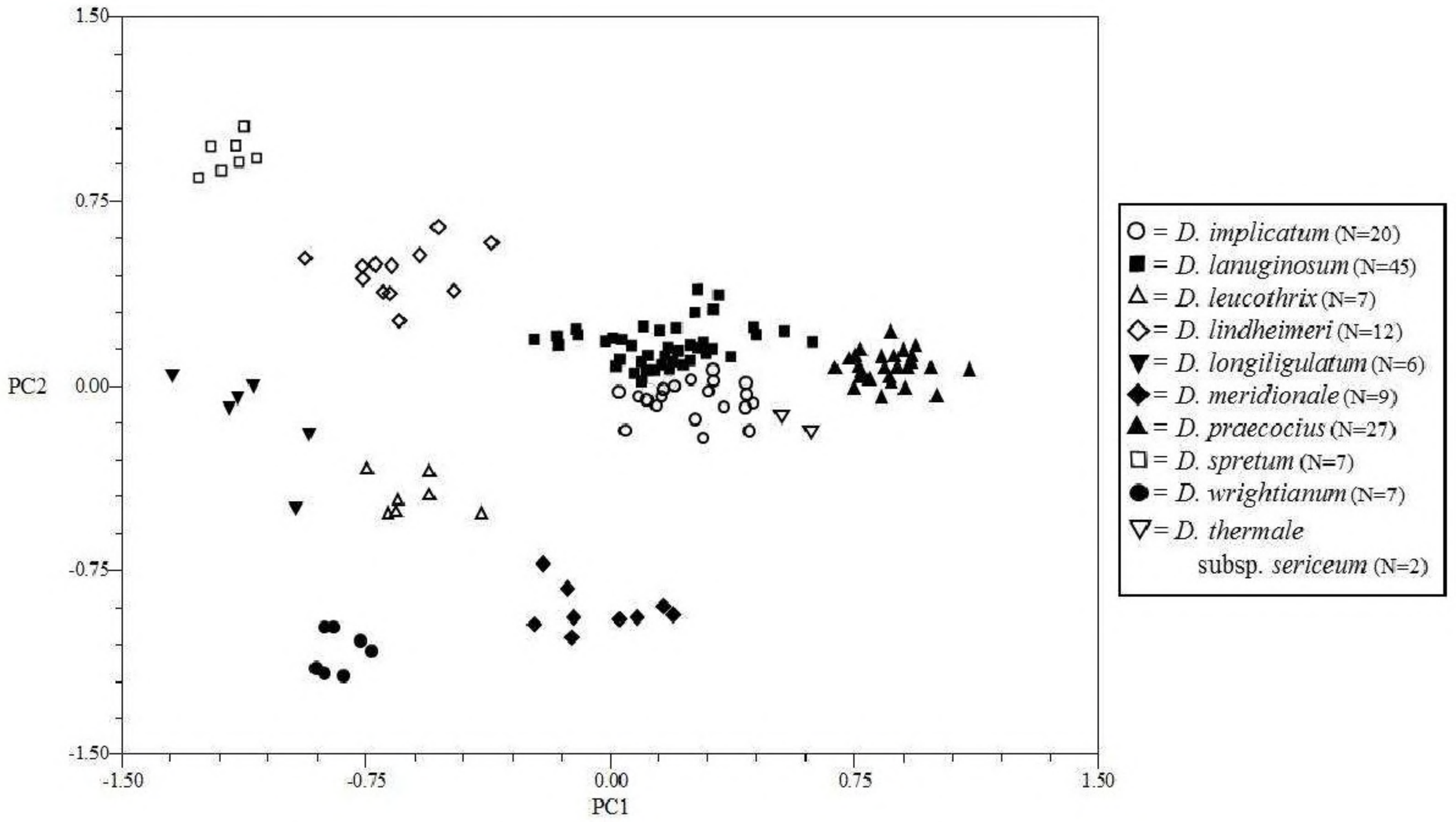


Figure 5. Scatter plot of the scores of principal component 1 (PC1) and principal component 2 (PC2) for all the standardized morphological characters of 142 specimens in the Long Ligule Group.

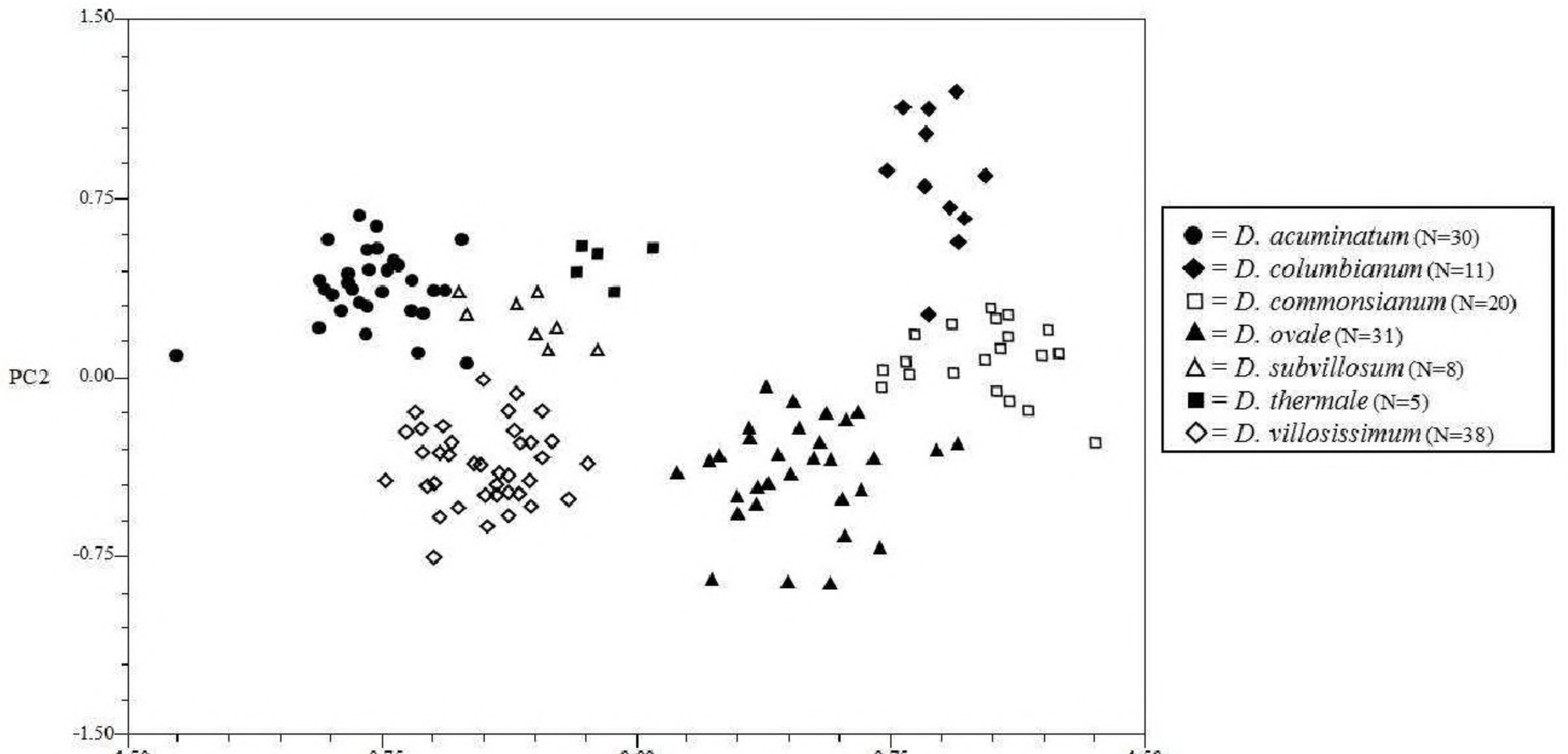


Figure 6. Scatter plot of the scores of principal component 1 (PC1) and principal component 2 (PC2) for all the standardized morphological characters of the 143 specimens in the Short Ligule Group.

	D. wrightianum	*D. spretum*	*D. meridionale*	*D. longiligulatum*	*D. leucothrix*	*D. implicatum*	*D. praecocius*	*D. lindheimeri*
D. lanuginosum	1,3,5,7,10,11,12, 13,14,15,**16**,17, 19,20,22,23	1,3,4,5,6,7,8,9, 10,**12**,15,16,18, 21,22,24	**1**,2,**3**,**5**,**10**,11, **13**,14,15,16,17, 19,20,23	**1**,4,3,5,6,7,8,**9**, 10,11,12,**13**,14,15, 17,18,**19**,20,22,23	**1**,2,3,**4**,**5**,6, 7,10,11,12,**13**, 14,15,20,22,23	5,**6**,7,9,10, **11**,**12**,14, 15,**16**	2,3,5,6,7,9, 10,11,12,13, 14,15,16,17	1,2,3,4,5,6, 7,8,9,10,**11**, 13,14,**15**
D. lindheimeri	**2**,4,6,7,8,9,10, 11,12,**13**,14,15, 17,18,19,20,22,23	**1**,**2**,**11**,**13**,**15**, 16,21,22,24	3,4,5,6,7,8,9,10, 13,14,15,**16**,17, 18,19,20,23	**2**,9,10,**11**,12, 14,15,20,22,23	4,7,8,9,10,11, 12,14,**15**,18, 20,22,23	**1**,2,3,4,5, 6,7,8,9,10, **13**,14,18	2,3,4,5,6,7, 8.9,10,11,12, 13,16,17,18	
D. praecocius	**1**,2,3,5,7,9,10, 11,12,13,14,15, 16,17,19,20,22,23	**1**,2,3,4,5,6,7,8, 9,10,11,12,13,**14**, 16,17,18,21,22,2 4	2,3,**5**,7,9,**10**,11, 12,13,14,15,16, 19,20,23	2,3,4,5,6,7,8,9,10, 11,12,13,14,15,16, 17,18,**19**,20,22,23	2,3,**4**,5,6,7,9,10, 11,12,13,14,**15**, 16,17,20,22,23	2,3,5,7,9, **10**,11,12, 13,14,16,17		
D. implicatum	**1**,3,5,7,9,10,11, 12,13,14,**15**,17, 19,20,22,23	1,3,4,5,6,7,8,9, 10,14,16,18,21, 22,24	2,**10**,13,**14**,15, **16**,17,19,20,23	3,4,5,6,7,8,9,10,**11**, 12,**13**,**15**,**17**,18, **19**,20,22,23	2,3,5,6,7,9,10, 11,12,14,20,22, 23			
D. leucothrix	2,3,6,7,11,12, 13,**14**,17,19	1,2,3,4,5,7,8,9,10 , 11,12,**13**,14,16, 18,20,21,23,24	3,5,6,10,11,12,13, **15**,16,17,19,22	2,3,4,5,7,8,**9**, **10**,**18**				
D. longiligulatum	**3**,4,6,7,8,**9**,**10**, 11,12,**13**,**14**,**17**, 18,19	**1**,**9**,**10**,11, **13**,14,**15**,20, 21,23,24	3,4,5,6,7,8,**9**,10, **11**,**12**,13,**16**,17, 18,19,22					
D. meridionale	**2**,3,5,7,10,11, 12,13,14,17,22	1,**2**,3,4,5,6,7,8,9, 10,**11**,14,15,16, 17,18,19,20,21, 22,23,24						
D. spretum	3,4,6,7,8,9,10,11, 12,13,14,**15**,16,17, 18,19,20,21,23,24							

Table 3. Results of pair-wise comparisons of Long Ligule Group using two sample t-tests. Numbers correspond to characters listed on Table 2. The numbers not in bold are those characters that demonstrate a significant difference of $P \leq 0.005$. Bold numbers are those characters that demonstrate P-values between 0.05 and 0.005.

	D. villosissimum	*D. thermale*	*D. subvillosum*	*D. ovale*	*D. commonsianum*	*D. columbianum*
D. acuminatum	**1**,11,13,30,31,32	13,25,26,31,32	**1**,13,15,**25**,26, **30**,31,32	1,11,13,26,27, 28,29,30,31,32	**1**,11,13,15,25, 26,27,28,29,31,32	1,13,15,25,26,27, 28,29,30, 31,32
D. columbianum	1,11,**13**,15,25,26, 27,28, 29,30,31	**1**,15,26,27,28,29,31	**1**,25,26,27,28, 29,30,31	1,11,13,15,25, 26,**27**,30,**31**	1,11,13,**27**,**30**	
D. commonsianum	1,11,13,15,25,26, 27,28, 29,30,31	11,13,15,26,27, 28,29,31	11,13,25,26,27, 28,29,31	1,13,15,25,26,27		
D. ovale	**1**,11,13,26,27,28, 29,30, 31	1,11,13,25, 26, 27,28,29,**30**,**31**	1,11,13,**15**,**25**,27, 28,29,**31**			
D. subvillosum	1,11,**15**,**25**,26,30	**15**,25,26,30				
D. thermale	**1**,11,25,26,30					

Table 4. Results of pair-wise comparisons of Short Ligule Group using two sample t-tests. Numbers correspond to characters listed on Table 2. The numbers not in bold are those characters that demonstrate a significant difference of $P \leq 0.005$. Bold numbers are those characters that demonstrate P-values between 0.05 and 0.005.

Variable	PC1	PC2	PC3
(1) LigLen	0.470134	0.013531	0.311942
(2) LigTriUni	0.367315	-0.044885	**-0.638994**
(3) MidShePubMax	**0.929179**	-0.051885	-0.166881
(4) MidSheGla	**-0.702810**	0.446930	-0.314728
(5) AdaLeaPubMax	**0.841107**	-0.131279	-0.102921
(6) AdaSurMidLeaGla	**-0.689265**	0.401993	-0.077478
(7) TerShePubMax	**0.882629**	0.027453	-0.135609
(8) TerSheGla	**-0.695017**	0.492033	-0.297461
(9) TerLeaAbaPubMin	**0.805324**	-0.174873	-0.234322
(10) TerLeaAbaPubMax	**0.852446**	-0.105936	-0.103876
(11) SpiLen	**0.653451**	0.549536	-0.320496
(12) SpiWid	**0.690557**	0.413550	-0.300294
(13) PriGluLen	**0.677986**	0.142037	-0.575833
(14) LonLeaLen	0.295223	**0.698455**	0.188139
(15) LonLeaWid	0.302144	0.469000	0.541051
(16) NumInfNod	-0.519752	0.389019	0.330314
(17) PubPubInf	-0.195249	**-0.727720**	-0.244033
(18) PedGla	**-0.651382**	0.533550	-0.295013
(19) PedPubDou	-0.271396	**-0.774095**	-0.179592
(20) AbaLeaSurPub	-0.496088	**-0.771455**	-0.188159
(21) InfNar	-0.455718	0.503179	-0.397369
(22) FerFloPoi	**-0.770360**	-0.162314	-0.227806
(23) InfDouVes	-0.471496	**-0.781279**	-0.181547
(24) SpiPoi	-0.455718	0.503179	-0.397369
total variance explained	39.8226%	20.1040%	11.6452%
eigenvalues	9.5574	4.8249	2.7948

Table 5. Loadings for the first three principal components from the PCA of the Long Ligule Group. Bold numbers are characters greater than 0.60 (absolute value).

Because what would be determined to be *Dichanthelium lanuginosum* and *D. implicatum* appeared to form two very close clusters with marginal overlap along PC1 and PC2 (Figure 5), a PCA of the data for just these two clusters was conducted in order to further focus on how morphologically similar or dissimilar they are to one another (Figure 7). T-tests for these two clusters demonstrated that *Dichanthelium lanuginosum* differs significantly ($P \leq 0.05$) from *D. implicatum* by 10 of the 24 characters sampled (Table 3). According to the t-tests, maximum leaf length, maximum leaf width and the length of pubescence on the abaxial surface of the terminal vernal leaf are the strongest characters separating *D. lanuginosum* and *D. implicatum*. The scatter plot of the first and second principal components (Fig. 7) demonstrate little overlap between these two taxa.

Within the Short Ligule Group, the first three principal component axes of the PCA accounted for 78 percent of the variation (Table 6). The first two principal component axes demonstrate seven clusters (Fig. 6). Distribution, orientation and density of pubescence, as well as glume length and characteristics of the ligule contributed the most variation along the first principal component. Ligule length and spikelet length contributed to the most variation along the second principal component.

Each cluster from the results of the SAHN cluster analyses and the PCAs of the Long Ligule and Short Ligule groups contained one or more type specimens. The taxonomic ranks and nomenclature applied in this treatment are based on the data analysis above, the type specimens contained within each cluster, the published descriptions of type specimens and comparison of those types not complete enough to be included in the general sampling. This followed a thorough review of all 160 published names and type specimens directly associated with these taxa as well as a comparison of the morphological limits derived from the data with 458 additional herbarium specimens from 33 states, 7 Canadian provinces, 4 Central American countries and 3 Caribbean islands. From these results, 16 species and one subspecies were found to best represent the morphological diversity found within sect. *Lanuginosa*. Lastly, a dichotomous key utilizing the strongest characters in the analysis was constructed. The key was found to efficiently differentiate the taxa when tested against the original 2780 herbarium specimens from throughout the range of sect. *Lanuginosa*.

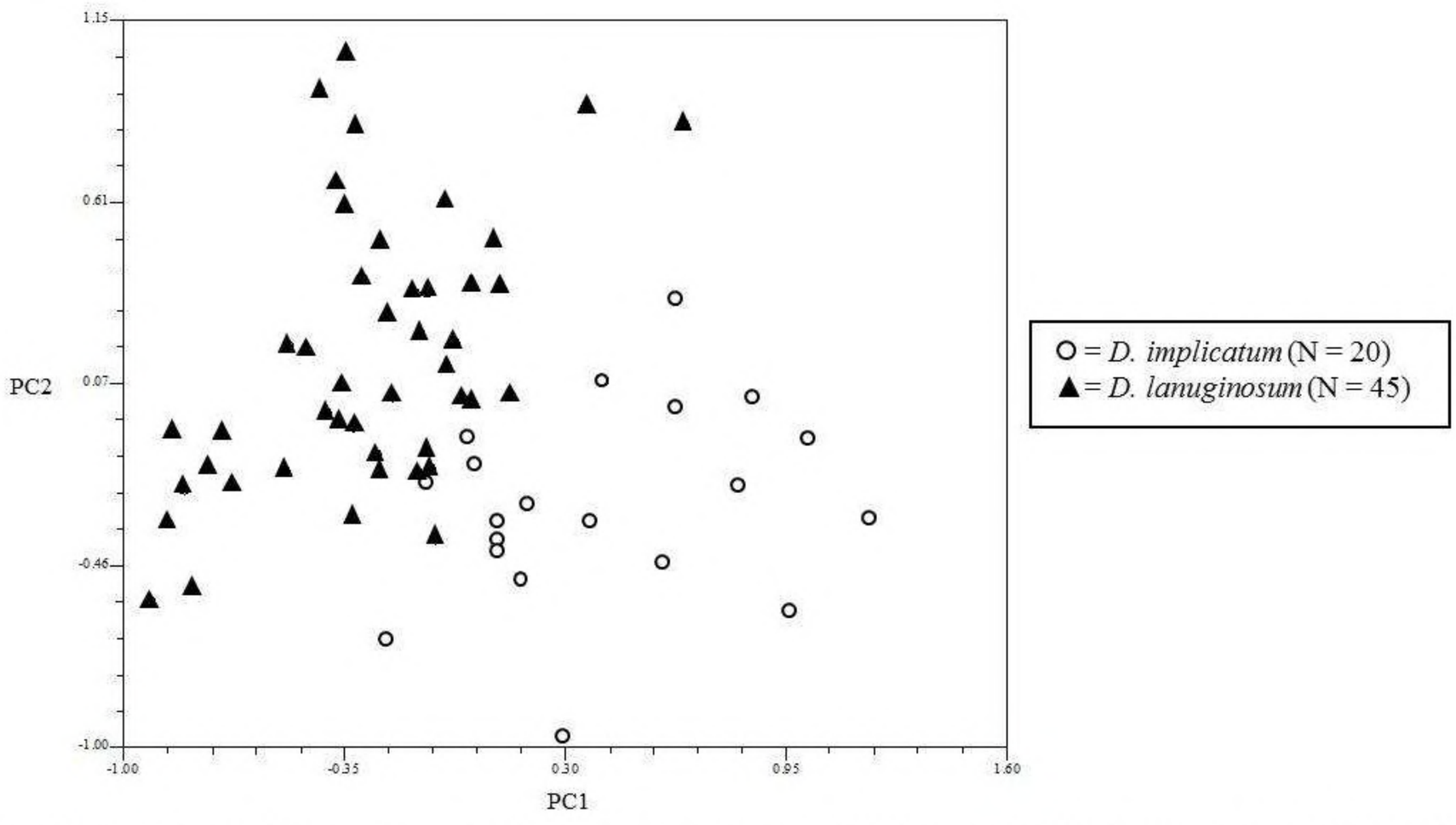


Figure 7. Scatter plots of the scores of principal component 1 (PC1) and principal component 2 (PC2) from PCA of *Dichanthelium implicatum* and *D. lanuginosum* specimens.

Variable	PC1	PC2	PC3
(1) LigLen	0.178984	**0.733770**	0.409249
(11) SpiLen	0.551986	**-0.754718**	-0.028215
(13) PriGluLen	**0.717599**	-0.486356	0.150821
(15) LonLeaWid	-0.501936	-0.259084	-0.311542
(25) DouLigCon	**0.670133**	0.481666	0.334808
(26) DouVes	**0.825638**	0.385092	0.202818
(27) NumTriAdaLeaSur	**-0.757211**	-0.061297	0.413394
(28) MidLeaGlaAda	**0.915842**	-0.061084	-0.259726
(29) TerLeaGlaAda	**0.915842**	-0.061084	-0.259726
(30) MidSheIndLen	-0.279299	**-0.648330**	0.569073
(31) ShePubOri	**-0.839872**	-0.016393	0.045759
(32) Cilia>30	-0.593963	0.447627	-0.458003
total variance explained	46.8454%	20.2014%	10.6903%
eigenvalues	5.6214	2.4241	1.2828

Table 6. Loadings for the first three principal components from the PCA of the Short Ligule Group. Bold numbers are characters greater than 0.60 (absolute value).

DISCUSSION

Based on the results of the SAHN cluster analyses, PCAs, the significance of each character in pairwise comparisons via t-tests, a complete review of the pertinent nomenclature, inclusion and review of the type specimens, and testing the assigned clusters against 2780 herbarium specimens from throughout the range of the group, sect. *Lanuginosa* is demonstrated to consist of at least 16 distinct species and one subspecies. Furthermore, based on herbarium label information, information provided in regional treatments, known phytogeographical trends, and the author's personal field experience, these taxa also prove to be ecologically and biogeographically satisfying.

While most of these taxa have recently been treated as subspecies or subsumed into synonymy, the entity level combinations of morphological, ecological, and geographical information provided here are interpreted as being more significant than can be justified by subspecific ranks. For example, the statistically distinct morphology expressed in what is here treated as *Dichanthelium praecocius* (*D. ovale* subsp. *praecocius* of Freckmann & Lelong 2003) is restricted to high quality prairie remnants within the Tallgrass Prairie Ecoregion while the statistically distinct morphology of what is here called *D. ovale* refers to an obligate acidophile restricted to the southeastern coastal plain of North America and the Antilles (see notes under *D. ovale* for a detailed discussion of the morphological differences in these taxa). Likewise, the morphological, ecological, and geographical distinctions of *D. thermale*, which only occurs along thermal springs of the Cascade and Rocky Mountains, provide more than sufficient evidence for recognizing *D. thermale* as a species as opposed to a subspecies (as in Freckmann & Lelong 2003) or synonym (as in Gould & Clark 1978) of *D. acuminatum*. Similar arguments are made under the notes section of each taxon.

While the splitting of the data into the Long Ligule Group and the Short Ligule Group was justified by the data analysis (Figures 1 and 2), it is important to note that it is also well in line with the interpretation and emphasis on ligule characters in several past treatments (Gould & Clark 1978; Hansen & Wunderlin 1988; Hitchcock & Chase 1910, 1951; Pohl 1947; Stone 1911). This split often correlates with the presence or absence of a distinct pseudoligule. Most members of the Long Ligule Group do not possess a distinct pseudoligule and many of the members of the Short Ligule Group possess a pseudoligule that is longer than the ligule. The exception to this occurs in glabrate forms of *Dichanthelium columbianum* and *D. ovale* (Short Ligule Group) where the lack of pubescence on the

adaxial leaf surfaces correlates to the lack of a pseudoligule. The ligule length character was also used in the treatments of Hitchcock and Chase (1910, 1951) as a major division between taxa in what is now considered section *Lanuginosa* such that the Long Ligule Group well represents most of the taxa included in the informal groups *Lanuginosa* and *Spreta* and the Short Ligule Group represents all members of *Columbiana* and a few members of *Lanuginosa*. It is also interesting that the geographical distributions of all members of the Long Ligule Group (minus the *Spreta* complex of Hitchcock and Chase which included what is here treated as *D. spretum*, *D. longiligulatum*, *D. leucothrix* and *D. wrightianum*) are mid-continental species that are largely absent from the coastal plain of southeastern USA while the Short Ligule Group and Hitchcock and Chase's *Spreta* are predominantly coastal plain species; most of which also range into the Antilles, Central America and northern South America. Furthermore, *Dichanthelium ovale*, *D. columbianum,* and *D. commonsianum*, the contemporary members of Hitchcock and Chase's *Columbiana*, are the only taxa to exhibit a restriction of pubescence to near the margins of the adaxial surfaces of vernal leaves (central portions glabrate). They also exhibit a double vestiture along vernal sheaths with puberulent pubescence often below a pilose or villose pubescence and ligules that are usually composed of intermeshed hairs of varying length. Given these morphological patterns and geographical affinities, further research investigating these trends within sect. *Lanuginosa* may find more credence in elevating the three informal groups recognized by Hitchcock and Chase to sectional status than maintaining the current, somewhat cumbersome, sect. *Lanuginosa*. Each of the individual phenograms for the Long Ligule Group (Figure 3) and Short Ligule Group (Figure 4) show two large divisions as well; also discernible in Figure 1. Three of these clusters are very well aligned with the original groups delineated by Hitchcock and Chase. The cluster containing *D. acuminatum*, *D. thermale*, *D. subvillosum,* and *D. villosissimum* could constitute a fourth section united by short ligule, dense pubescence, a lack of puberulence, and spikelets around 2mm long.

Given the large morphological, ecological and geographical ranges of some of the species delimited in this treatment and the relatively few representative specimens of each within the dataset, there is reason to suspect that there may be other taxa, some potentially valid species, that were not detected in the analysis. For example, while *Dichanthelium thurowii* and *D. auburne* are here maintained in the synonymy of *D. acuminatum*, the specimens in the analysis, including the type material, coupled with the descriptions and the geographical ranges reported by Hitchcock and Chase (1910, 1950) suggest that the taxonomic clarity of *D. acuminatum* sensu stricto may be under-investigated. Also, the type specimen of *P. pseudopubescens* and the corresponding morphology could not be completely differentiated from the *D. villosissimum* clade on the phenogram and PCA cluster. A review of specimens raised enough questions that the morphological limits of this potential entity should be more thoroughly reviewed (see notes under *D. villosissimum*). The same can be said for what are treated here as *D. implicatum*, *D. lanuginosum*, *D. lindheimeri*, and *D. thermale* in that each appear to contain morphological expressions that correlated to different habitats and geographical ranges (see the taxonomic notes of each species for details). In each of these cases, more field work and data analysis are needed to determine whether these more cryptic morphologies are taxonomically meaningful.

Long Ligule Group

The results of the phenetic analysis (Figure 3), PCA (Fig. 5 and Table 5) and t-tests (Table 3) defend the segregation of ten entities that are here interpreted as nine species and one subspecies in the Long Ligule Group. With the exception of some subtlety between *Dichanthelium lanuginosum* and *D. implicatum*, all taxa in the Long Ligule Group demonstrated clear morphological distinction. While the phenetic analysis (Figure 3) showed considerable separation between *D. lanuginosum* and *D. implicatum*, there was some degree of overlap between the two in the scatter plots of the PCA (Figure 5). A second PCA involving only *D. lanuginosum* and *D. implicatum* (Fig. 7) further confirmed that, while these two taxa are morphologically similar, they are distinct and several other

studies (Allen 2001; Naczi 1998; Peterson et al. 2002; Rothrock & Reznicek 2001; Saarela et al. 2003; Binns et al. 2002) have used similar levels of distinction for separating closely related taxa as distinct species. Furthermore, *D. lanuginosum* significantly differs from *D. implicatum* ($P \leq 0.05$) by 10 of the 24 characters sampled (Table 5). Maximum leaf length, maximum leaf width, and the length of pubescence on the abaxial surface of the terminal vernal leaf are the strongest characters separating these two taxa. Given the distinctness of the majority of specimens and the narrower ecological niche of *D. implicatum* (restricted to acidic substrates in woodland habitats) these taxa are here treated as separate species.

The analysis did not well describe the full complement of morphological variation found within the *Dichanthelium thermale* complex. Specimens that have always been associated with the complex were found in both the Long Ligule and Short Ligule groups. Essentially, the data demonstrated that what is here called *D. thermale* subsp. *thermale* clearly possesses a short ligule backed by a longer pseudoligule and is only found along hot springs in northern California. What is here called *D. thermale* subsp. *sericeum* possesses a long ligule and only occurs near hot springs and geysers in the Rocky Mountains. However, a few specimens (such as the type for *P. ferventicola*) from Yellowstone National Park have intermediate ligule lengths and specimens from Banff, Alberta, (such as the type for *P. ferventicola* var. *papillosum*) have very short and wide leaves. As noted by Hitchcock and Chase (1910), pubescence characters and leaf dimensions for the *P. thermale* complex are variable across its range. Given this range of variability, the *D. thermale* complex was interpreted more from the raw data and a review of specimens than from the analysis (see notes under *D. thermale* for details). This resulted in the recognition of *D. thermale* subsp. *thermale* and subsp. *sericeum*, which is similar to the treatment of Freckmann and Lelong (2003). *Dichanthelium thermale* has been found to be dependent on a triple mutualism between a fungal endophyte and a viral symbiont, which provide it with remarkable thermal tolerance (Marquez et al. 2006). The uncertainty of the effect of this three-way mutualism on the morphology of these plants, coupled with the island-like distribution of their populations, necessitates a more detailed study than can be provided here.

While the PCA, phenetic analysis, and t-tests demonstrate strong differences between *Dichanthelium lanuginosum* and *D. lindheimeri*, the application of morphological characters to specimens can be challenging. Much of the separation generated in the analyses above originates from pubescence characters, where *D. lindheimeri* is mostly glabrous and *D. lanuginosum* is always pubescent. The two taxa are very similar especially when sparsely pubescent specimens of *D. lanuginosum* are encountered (see notes under *D. lindheimeri* for details on distinguishing these taxa). This similarity has led some authors to lump these taxa or treat one as a subspecific taxon of the other. Because of its glabrosity, *D. lindheimeri* is more closely linked with *D. spretum* in the PCA and phenetic analysis. While this may seem wholly artificial, plants from calcareous lake shores in the Great Lakes region (Voss 1972; Voss & Reznicek 2012) that are here treated as *D. lindheimeri* are morphologically similar to *D. spretum*. Said plants have the overall stature of *D. spretum* coupled with pubescence and floral characters more aligned with *D. lindheimeri* (for details see notes under *D. lindheimeri*). In the phenetic analysis the more sparsely pubescent specimens of *D. lanuginosum* sorted together in a branch of *D. lanuginosum*. These specimens represent what has been called *P. tennesseense* and *P. lindheimeri* var. *septentrionale*. Following a review of these OTUs, as well as numerous additional herbarium specimens, no clear distinction could be found to justify maintaining this cluster as an infraspecific taxon. The phenetic analysis likewise demonstrated other small, seemingly distinct, groups in the *D. lanuginosum* and *D. praecocius* branches. Upon investigation of these groups, no justification for subspecific separation could be found, based on morphology. This is not to say, however, that such distinctions do not exist.

Short Ligule Group

In the Short Ligule Group, the results of the phenetic analysis (Figure 4), PCA (Figure 6 and Table 6) and t-tests (Table 4) demonstrate the segregation of seven entities that are here interpreted as distinct species. One outlier within the *Dichanthelium columbianum* cluster in Figure 4 represents the type specimen of *P. scoparioides*. This specimen possesses all the traits of typical *D. columbianum* except for its larger spikelets. This is interpreted as the extreme maximum of the phenotypic plasticity found within *D. columbianum* rather than a distinct taxon. Gould and Clark (1978) placed *P. scoparioides* into synonymy under their broad interpretation of *D. acuminatum*. However, using their key and descriptions, the type specimen better fits their *D. sabulorum* var. *thinium* which is here treated as a synonym of *D. columbianum* (typical *D. sabulorum* and var. *patulum* are now under *D. portoricense* in section *Lancearia*). Freckmann and Lelong (2003) referred to *P. scoparioides* as being a sterile hybrid between *D. oligosanthes* and their broad interpretation of *D. acuminatum* (which includes *D. columbianum* of the present treatment). The possibility of *P. scoparioides* being a hybrid does not seem unreasonable. Given the numerous specimens reviewed throughout the range of *D. columbianum* it is abundantly clear that the spikelet length demonstrated by *P. scoparioides* is a rare exception to the otherwise narrow morphological range of *D. columbianum* for this character.

Similarly, one outlier within the *Dichanthelium acuminatum* cluster (Figure 4) represents the type specimen of *P. comophyllum*. It falls outside the main cluster due to its wider leaves and more densely pubescent adaxial leaf surfaces. Hitchcock and Chase (1910) and Gould and Clark (1978) treated it as a synonym of *P. acuminatum*, while Freckmann and Lelong (2002, 2003) did not include any mention of its placement within the section. Because this is a solitary specimen that does not currently appear to match any common morphological theme within the group, it is interpreted here as an aberrant specimen that is not characteristic of the more uniform morphology expressed by *D. acuminatum*.

According to the phenetic analysis and PCA, what is here treated as *D. subvillosum* is most similar to *Dichanthelium thermale* and *D. acuminatum*, though their geographic ranges and habitats differ strikingly. *Dichanthelium thermale* has a double vestiture of pubescence on the basal and lower leaf sheaths of the vernal culm, shorter pubescence on vernal sheaths, and only occurs in moist geothermal soils of the Cascade and Rocky Mountains. *Dichanthelium subvillosum* has a single vestiture throughout the vernal culm, a longer pubescence on the vernal sheaths, and does not occur in the habitat or near the altitudes of *D. thermale*. The geographical ranges of both *D. thermale* and *D. subvillosum* are restricted to northern North America while the range of *D. acuminatum* is limited to the coastal plain of the southeastern USA, Gulf of Mexico, and into South America (for details see notes under *D. thermale* and *D. subvillosum*).

The phenetic analysis of the Short Ligule Group shows some small groups within the larger branches of *Dichanthelium acuminatum* and *D. villosissimum*. It seems probable that there is some level of taxonomic resolution to be found in these subordinate groups, but they are below the threshold of distinction given the methodology of this study. Future investigations into the details of these species are certainly in order.

Relevance to Past Studies

The present study confirms that the treatment of Hitchcock and Chase (1910), with its recognition of 33 species and two varieties within what is now sect. *Lanuginosa*, over-emphasized the measurable morphological diversity found within the section. The plethora of names associated with the section is demonstrative of the inherent morphological variability within the group. Slow rates of communication between nineteenth-century botanists also contributed to an over-naming (160 names are currently associated with sect. *Lanuginosa*). Subsequent treatments, such as Gould and Clark (1978) and Freckmann and Lelong (2002, 2003), have attempted to narrow the taxonomic limits

within the section but have underestimated the morphological evidence that here justifies maintaining many of these taxa above the subspecific rank.

The most obvious difference between the current treatment and those of Gould and Clark (1978) and Freckmann and Lelong (2002, 2003) is the circumscription of *Dichanthelium acuminatum*. In the treatment of Gould and Clark (1978), 13 of the 15 species in the present treatment are placed into 8 varieties under *D. acuminatum*. They qualified their treatment with the statement "It may be that the taxa retained as varieties do not adequately delimit the recognizable populations of this extremely widely distributed and morphologically variable species." The treatment of Freckmann and Lelong (2003) placed 10 of the 15 species recognized in the present treatment into 10 subspecies of *D. acuminatum*. They stated that morphologically intermediate specimens derived from hybridization and autogamy produce "a reticulate pattern of intergradation between members of the section [*Lanuginosa*]." While introgression, hybridization, and autogamy could offer mechanisms for intermediate morphologies, such phenomena have not been systematically proven to exist in *Dichanthelium* and the present study failed to find a significant number of morphologically intermediate specimens. Of the nearly 3000 specimens reviewed during the present treatment, the vast majority were easily placed into the taxa as outlined below. In direct reference to their broad circumscription of *D. acuminatum* Freckmann and Lelong (2003) stated that "there appears to be widespread introgression from other *Dichanthelium* species, such as *D. dichotomum, D. sphaerocarpon, D. ovale*, and *D. aciculare*." The very few instances where specimens in this study were difficult to distinguish usually occurred where what appeared to be closely related species came into contact on the edges of their ranges. For example, along the southern tip of Lake Michigan where the northeastern terminus of the Tallgrass Prairie Ecoregion meets the sandy soils of the black oak savannas of northern Illinois and Indiana, *D. praecocius* and *D. villosissimum* can be difficult to differentiate and are suggestive of some level of introgression. However, such putatively intergrading specimens are rare and do not warrant expunging the taxonomic, ecological, and biogeographical relevance that maintaining these entities as distinct species otherwise provides throughout the vast majority of their ranges. This level of what is often interpreted as hybridization or introgression is both acceptable and even expected in other complex groups (*Symphyotrichum*, *Solidago*, *Carex*, *Quercus*, etc.) without the dissolution of species with an otherwise high morphological fidelity and geographical predictability throughout the majority of their respective ranges. When such rare hybrid events, the mechanisms and consequences for which we do not fully understand, are used to justify the subsumption of taxa, we deny ourselves access to the real-world expressions of evolutionary development, function, and existence, as well as the chance to celebrate them. These hybrid moments should be described and named and not misconstrued as mortar in an imaginary wall of taxonomic reticulation.

Gould and Clark (1978) initiated, and Freckmann and Lelong (2002, 2003) maintained, a broad interpretation of *D. ovale*, though the two treatments differ significantly. Gould and Clark (1978) placed what is here treated as *Dichanthelium commonsianum* as a variety of *D. ovale* (var. *addisonii*, which is placed in synonymy with *D. columbianum* in the present treatment) and maintained the typical variety to represent what had traditionally been *D. ovale*. The basis of that treatment, as gleaned from their keys, seems to be the presence of a double vestiture on the vernal sheaths, longer spikelets, and the distribution of pubescence along the adaxial surface of vernal leaves. While the present study failed to confirm any differences in adaxial leaf pubescence or spikelet length, the presence and extent of a double vestiture along the vernal sheaths did prove informative. Freckmann and Lelong (2002, 2003) proposed an even broader interpretation of *D. ovale* that includes *D. villosissimum* and *D. praecocius* (as subsp. *villosissimum* and subsp *praecocius*) and incorporated *D. commonsianum* into subsp. *pseudopubescens* (see notes under *D. ovale* for details). In their treatment of *D. ovale*, Freckmann and Lelong (2002, 2003) and Lelong

(1984) are the only authors to combine taxa from the informal groups *Columbiana* and *Lanuginosa* of Hitchcock and Chase (1910).

Like the present treatment, Freckmann and Lelong (2003) maintained *Dichanthelium wrightianum* as a distinct species. However, Gould and Clark (1978) chose to place *D. wrightianum* as a variety of *D. acuminatum*. Given its diminutive stature and consistently tiny spikelets (0.8 to 1.0 mm long), there should be little debate regarding the distinct nature of this taxon. It is difficult to envision it being treated as anything other than a substantiated species.

Though it is not always a primary concern of taxonomy, the conservation status, political protection, and ultimately the degree of intellectual investment from field biologists that rarely interest themselves in a regional flora below the level of species are greatly affected by the ultimate utility of taxonomy. Recognizing ten subspecies under *Dichanthelium acuminatum* is not only taxonomically unsatisfying but it also diminishes the potential for protecting such conservative and regionally imperiled species as *D. columbianum*, *D. longiligulatum*, *D. praecocius*, *D. meridionale*, *D. spretum*, and *D. thermale*. It is a matter of opinion, but if there is any question as to the distinctness of these entities as isolated evolutionary lineages, taxonomists are obligated to err on the side of caution and maintain such taxa as species until we better understand their significance rather than learn too late that we too eagerly dismissed their uniqueness.

Sources of confusion

Much of the past confusion within sect. *Lanuginosa* originates from the varying interpretations of taxonomically useful characters. Most treatments have relied heavily on spikelet length, the length of the ligule, and characters involving the indument. The present study has also found that these traits provide clarity but only for certain species and in conjunction with other characters. Furthermore, when applied to the section, characters like spikelet length, double ligule, and double vestiture require a more detailed characterization than most treatments provide. Spikelet length in the present treatment is defined as the length of the spikelet from the base of the first glume to the tip of the second glume. Where possible the most mature spikelets of the vernal inflorescence should be used. Immature spikelets and those of the autumnal inflorescence are often highly variable and can result in inconsistent measurements.

Characterization of the diverse expressions in the ligule length, shape, and uniformity can also be problematic. Members of the Long Ligule Group, such as *Dichanthelium lanuginosum* and *D. implicatum*, possess a "single ligule," which means there is no pseudoligule or that the hairs of the ligule and the pseudoligule are of the same length and thereby not discriminable (Fig 8a). This is in contrast to members of the Short Ligule Group like *D. ovale* and *D. columbianum*, which often have a "double ligule" or a distinct pseudoligule, where the true ligule is composed of short hairs and the pseudoligule is composed of longer hairs behind the ligule. The hairs of the pseudoligule originate from the immediate adaxial leaf surface (Figure 8b). Adding to the confusion, some taxa that typically have a longer pseudoligule occasionally lack it (corresponding to glabrous adaxial leaf surfaces) and thus appear to possess a "single" short ligule (Figure 8c). In herbarium specimens, distinguishing the ligule and pseudoligule can often be problematic because the ligule and pseudoligule (when both are present) may become intermeshed during the drying process (Figure 8d). One would think this a simple matter, but several of the type specimens reviewed for this project possessed a ligule type that differs significantly from that in the author's original description (included ligule and pseudoligule in original measurements for "ligule," for example). In the present treatment the key to taxa breaks from this traditional terminology by referring only to the first row of ligule hairs. This avoids the confusion associated with ligule and pseudoligule and focuses attention on the relevant issue of whether the immediate hairs (first row) are long or short.

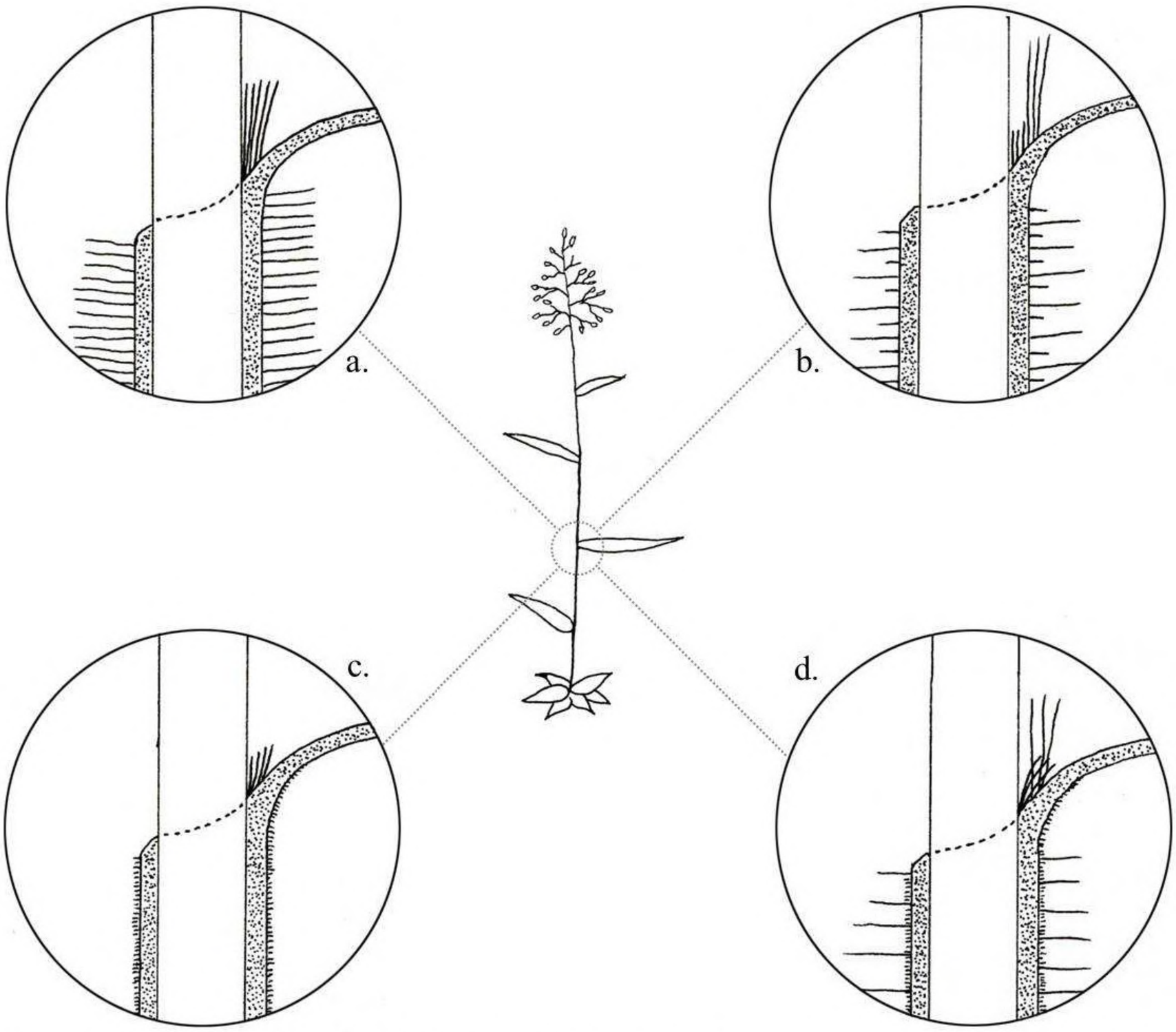


Figure 8. Examples of the four ligule types and the four pubescence types found within section *Lanuginosa*. All combinations of the eight illustrated characters are possible. **Ligule illustration a.)** occurs in *D. implicatum*, *D. lanuginosum*, *D. leucothrix*, *D. lindheimeri*, *D. longiligulatum*, *D. meridionale*, *D. praecocius*, *D. spretum*, *D. thermale* subsp. *sericeum* and *D. wrightianum*; **b.)** occurs in *D. acuminatum*, *D. columbianum*, *D. commonsianum*, *D. ovale*, *D. subvillosum*, *D. thermale* and *D. villosissimum*; **c.)** occurs in *D. columbianum*, *D. commonsianum* and *D. ovale*; **d.)** occurs in *D. acuminatum*, *D. columbianum*, *D. meridionale*, *D. subvillosum*, *D. thermale* subsp. *sericeum* and *D. thermale* subsp. *thermale*. **Pubescence illustration a.)** occurs in *D. acuminatum*, *D. implicatum*, *D. lanuginosum*, *D. praecocius*, *D. thermale* subsp. *sericeum* and *D. villosissimum*; **b.)** occurs in *D. acuminatum*, *D. subvillosum*, *D. thermale* subsp. *thermale* and *D. villosissimum*; **c.)** occurs in *D. columbianum*, *D. commonsianum*, *D. leucothrix* and *D. wrightianum*; **d.)** occurs in *D. columbianum*, *D. commonsianum*, *D. leucothrix*, *D. meridionale*, *D. ovale*, *D. thermale* subsp. *thermale* and *D. wrightianum*.

Another character state that has caused confusion in the group is the presence or absence of a "double vestiture" in reference to sheaths, internodes, peduncles, and the axes of the inflorescences. This is problematic because two types of double vestiture are possible for taxa in sect. *Lanuginosa*. First, taxa that typically have a single vestiture of long pilose hairs (Fig. 8a) can occasionally have an additional indument of short pilose hairs (Fig. 8b). Second, some taxa have long pilose hairs above short puberulent hairs (Fig. 8d). In the latter case, some specimens can lack the longer pilosity (Fig. 8c) and thus do not truly have a "double vestiture." All previous treatments that have utilized the "double vestiture" character to distinguish taxa have failed to define these subtleties. To avoid this confusion in the present treatment, any reference to "double vestiture" includes a description of whether the subordinate pubescence is pilose or puberulent. Because the distinguishing features of

the ligule, spikelet, and sheath pubescence can be minute, a minimum of 30X magnification is required to fully discern the differences in taxa. Furthermore, all measurements regarding these characters should be taken with calipers or a sub-millimeter scale while under a dissecting scope.

Because the morphology of the autumnal branches and inflorescences often differ strikingly from that of the vernal culms and inflorescences, all key characters in the present treatment are in reference to the vernal culm. The autumnal branches, leaves, and inflorescences of most taxa in the section become highly fascicled and finely pubescent late in the summer. This is often accompanied by the senescence of the vernal stem leaves. Thus, plants collected late in the season become increasingly difficult to identify. The exceptions to this are *Dichanthelium implicatum* and *D. columbianum*, both of which have the distinct feature of the vernal leaves curling under into a nearly circular configuration. No other members of the section do this. As the collector of *Carex* must be mindful of the shattering of perigynia from the spike, the collector of *Dichanthelium* should seek specimens that possess fresh components of the vernal stem and thus the full complement of morphological expression.

The most problematic source of confusion in sect. *Lanuginosa* is the relationship of *Dichanthelium lanuginosum* and *D. acuminatum*. Much of this confusion seems to stem from the regional misapplication of names. *Dichanthelium acuminatum*, long considered a species of the Caribbean, was not considered to be an element of the flora of North America until the treatment of Gould and Clark (1978). It appears to have been mistakenly called *Panicum lanuginosum* prior to this clarification (Hitchcock & Chase 1910; Small 1903, 1933). The name *P. lanuginosum* was also being applied, correctly so, to plants of the interior of North America. In 1910, Hitchcock and Chase designated the name *P. lanuginosum* to plants of the southern coastal plain and relegated the plants of the interior to *P. huachucae*. Finding little to no difference between specimens of *P. huachucae* and earlier published names such as *P. lindheimeri* and *P. implicatum* (*Dichanthelium lindheimeri* and *D. implicatum* of the present treatment), the regional treatments of Fernald (1922), Pohl (1947), Shinners (1944), Voss (1972), and Swink and Wilhelm (1994) utilized these earlier names for plants in their respective regions. Fernald (1934, 1950), attempted to correct this discrepancy and realigned these taxa with *P. lanuginosum* by placing *P. lindheimeri*, *P. implicatum*, as well as other species, as varieties of *P. lanuginosum* while restricting the typical variety to the southern coastal plain (apparently still in reference to what we now call *D. acuminatum*). In Fernald's realignment, *P. lanuginosum* var. *fasciculatum* (of which *P. huachucae* is a synonym) came to represent the most wide-ranging taxon of the section in the interior of North America. In 1978, Gould and Clark became the first authors to include *D. acuminatum* into the flora of North America. However, instead of maintaining *D. lanuginosum* as distinct from *D. acuminatum* they placed it and all the above-mentioned taxa, plus several others, into synonymy with *D. acuminatum*. A similar arrangement was maintained by Freckmann and Lelong (2002, 2003).

While inclusion of *Dichanthelium acuminatum* in the North American flora helped clarify this issue, the placement of *D. lanuginosum* in synonymy with *D. acuminatum* is not justified by the findings of this study. In fact, for reasons mentioned throughout, morphological, ecological, geographical, and taxonomic clarity is maximized by extracting *D. lanuginosum* from *D. acuminatum*. The type of *D. lanuginosum* is more velvety pubescent than most of the more western specimens of the taxon — so much so that one wonders if it may actually represent a more eastern cryptic expression. In this case the western expression becomes better aligned with *P. huachucae* of Hitchcock and Chase (1910, 1951), *P. lindheimeri* of Fernald (1922), *P. implicatum* of Pohl (1947) and Voss (1972), and *P. lanuginosum* var. *fasciculatum* of Fernald (1934, 1950) and Gleason and Cronquist (1991). Should future studies find a stronger difference between the coastal and interior manifestation of *P. lanuginosum*, those of the interior would be relegated back to either Fernald's var. *fasciculatum* or the species "*huachucae.*"

Confusion also has risen from taxa outside sect. *Lanuginosa*. Specimens of *Dichanthelium consanguineum* (sect. *Angustifolia*) and *D. laxiflorum* (sect. *Strigosa*) are commonly encountered in the herbarium folders of taxa from sect. *Lanuginosa* as misidentifications. *Dichanthelium consanguineum* differs from all members of sect. *Lanuginosa* in having attenuate spikelets and thin primary glumes. Because it often has a light puberulence on the culm, it is often confused with *D. ovale* or *D. commonsianum*. *Dichanthelium laxiflorum* differs in having longer winter rosette leaves and culm leaves that are more basally disposed. It often has more of a yellow-green coloration, a smaller ligule, and more extensive cilia on the leaf margins than members of sect. *Lanuginosa*. It most resembles *D. acuminatum* and *D. villosissimum*.

TAXONOMIC TREATMENT

Dichanthelium sect. ***Lanuginosa*** (Hitchc.) Freckmann & Lelong. **Plants** caespitose, 5–120 cm, glabrous to densely pilose, villose or puberulent. **Basal rosettes** conspicuous and over-wintering. **Culms** erect early in the season, often sprawling later. **Leaves** evenly distributed along the culm, almost always less than 1 cm wide. **Ligules** a dense ring of hairs, 0.2–5.0 mm long, often backed by a pseudoligule. **Spikelets** 0.8–3.0 mm long, elliptic to ovate-elliptic, pubescent, the first glume ¼ to ½ the spikelet length, the second glume and sterile lemma 5–9 nerved.

1. First row of ligule hairs ≥ 1.7 mm long (key intermediate specimens here).

    2. Surfaces of distal and midstem leaf sheaths of vernal culms glabrous or glabrate (ignore hairs restricted to the sheath margins).

        3. Inflorescence < 1/3 as wide as long; spikelets acute to attenuate at the apex and ovate to lanceolate in outline; leaves and sheaths rigid with a stiff, smooth texture; inflorescences densely flowered; collar region of vernal leaves eciliate ..... **Dichanthelium spretum**
        3. Inflorescences at least ½ as wide as long; spikelets obtuse at the apex and elliptic to elliptic-ovate in outline; leaves and sheath thin with a papery texture; inflorescences sparsely flowered; collar region of vernal leaves most often ciliate.

            4. Spikelets 1.3 – 1.7 mm long; base of proximal vernal stem leaves with marginal cilia; largest leaves of the vernal culm typically > 60 mm long and 5 mm wide (similar to the proportions of *D. lanuginosum*); stems thickish and with typical autumnal fascicles ..... **Dichanthelium lindheimeri**
            4. Spikelets usually 1.1 – 1.5 mm long; base of proximal vernal stem leaves usually lacking marginal cilia or restricted to less than three hairs per side; largest leaves of the vernal culm typically < 60 mm long and 5 mm wide; stems wiry with autumnal fascicles dense and pom-pom like ..... **Dichanthelium longiligulatum**

    2. Surfaces of distal and usually midstem leaf sheaths of vernal culms pubescent with a uniform indument of variable density (note: some taxa possess a very short puberulence of hairs between the veins of the sheath that require 10X magnification).

        5. More than 30 cilia on each margin of the middle and lower leaves of the vernal culm; marginal cilia extending from the base of the leaves to approximately half way up the blade ..... **Dichanthelium acuminatum** (in part)
        5. Less than 20 cilia on each margin of the middle and lower leaves of the vernal culm; marginal cilia restricted to the basal ¼ of the blade.

            6. Plants restricted to hot geothermal soils of the Cascade and Rocky Mountains.

7. Largest vernal stem leaves < 8 mm wide; pubescence on the vernal sheaths < 2.0 mm long ..... **Dichanthelium thermale** subsp. **thermale** (in part)
7. Largest vernal stem leaves > 8 mm wide; pubescence on the vernal sheaths > 2.0 mm long ..... **Dichanthelium thermale** subsp. **sericeum**

6. Plants never growing in hot geothermal soils.

8. Upper surface of mid-stem leaves of vernal culms lacking pubescence along the central one third of the blade from base to tip .. **Dichanthelium columbianum** (in part)
8. Upper surface of mid-stem leaves of vernal culms uniformly pubescent across the surface (margin to margin) or glabrous.

9. Plants with a puberulent pubescence (less than 0.3 mm long) on the under surfaces of vernal stem leaves; main axis of the inflorescence possessing a puberulent pubescence often beneath longer pilose hairs; largest vernal leaves 22–65 mm long; spikelets often puberulent.

10. Spikelets ≤ 1.1 mm long and 0.5 mm wide ..... **Dichanthelium wrightianum**
10. Spikelets ≥ 1.2 mm long and 0.5 mm wide.

11. Longer hairs of the mid-stem sheaths and the upper leaf surfaces of vernal stem leaves ≤ 2 mm long; other than occasional puberulence, upper surface vernal stem leaves with sparse pilosity or lacking pilosity; almost exclusively a species of coastal regions from New Jersey south through the Gulf of Mexico to northern South America and the Antilles ..... **Dichanthelium leucothrix**
11. Longer hairs of the mid-stem sheaths and the upper leaf surfaces of vernal stem leaves mostly > 2 mm long the upper surface of vernal leaves conspicuously pilose; a species of southern Canada and the northern USA south to Georgia and Alabama including coastal and inland regions ..... **Dichanthelium meridionale**

9. Plants lacking hairs or with a velutinous, pilose or hispid pubescence on the under surfaces of vernal stem leaves; main axis of the inflorescence lacking a puberulent pubescence; largest vernal leaves 40–110 mm long; spikelets not puberulent.

12. Spikelets 1.8–2.1 mm long; first glume 0.7–1.0 mm long; longest hairs of the mid-stem vernal sheaths mostly 2.7–4.5mm long; often 10 or fewer nodes along the central axis of the inflorescence; ligule a mixture of long and short hairs with shorter hairs more abundant in the center thereby creating a U-shaped ligule in general outline; leaves often ascending; endemic to the Tallgrass Prairie Ecoregion ..... **Dichanthelium praecocius**
12. Spikelets 1.3–1.8 mm long; first glume 0.3–0.7 mm long; longest hairs of the mid-stem vernal sheaths usually < 2.7 mm long; usually 12 or more nodes along the central axis of the inflorescence; ligule hairs approximately the same length throughout; leaves spreading; widespread.

13. Largest vernal leaves typically ≤ 65 mm long; vernal stem leaves typically < 6.0 mm wide; plants growing in acidic substrates and usually at sites with significantly high native floristic quality; typical habitats include sandy or cherty woodlands, prairies and glades as well as bogs, cedar swamps, tamarack swamps ..... **Dichanthelium implicatum**

13. Largest vernal leaves typically > 65 mm long; vernal stem leaves typically > 6.0 mm wide; plants more often associated with neutral or alkaline soils and not indicative of high native floristic quality; typical habitats include old fields, woodlands, prairies and glades ..... **Dichanthelium lanuginosum**

1. First row of ligule hairs ≤ 1.5 mm long.

14. Upper surfaces of vernal stem leaves glabrous or glabrate along entire blade

15. Lower and basal sheaths possessing a single indument of long villose pubescence and lacking an additional short puberulence (occasional specimens may have pilose hairs under the villose hairs) ..... **Dichanthelium villosissimum** (in part)
15. Lower and basal sheaths possessing a double vestiture of long pilose or villose pubescence above a short puberulence or only possessing a short puberulence.

16. Spikelets ≤ 2.1 (rarely to 2.4) mm long; ligule usually > 1 mm long; first glume ≤ 1 mm long ..... **Dichanthelium columbianum** (in part)
16. Spikelets > 2.1 mm long; ligule usually ≤ 1 mm long; first glume typically > 1 mm long

17. Distal sheath of vernal culms possessing a short puberulence (often below longer or villose hairs); ligule of vernal stem leaves > 0.7 mm long ..... **Dichanthelium commonsianum** (in part)
17. Distal sheath of vernal culms glabrous, pilose or villose but lacking a short puberulence; ligule of vernal stem leaves < 0.7 mm long ..... **Dichanthelium ovale** (in part)

14. Upper surfaces of vernal stem leaves conspicuously pubescent.

18. Upper surface of mid-stem leaves of vernal culms uniformly pubescent across the surface (margin to margin).

19. More than 30 cilia on each margin of the middle and lower leaves of the vernal culm; marginal cilia extending from the base of the leaves to approximately half way up the blade ..... **Dichanthelium acuminatum** (in part)
19. Less than 20 cilia on each margin of the middle and lower leaves of the vernal culm; marginal cilia restricted to the basal ¼ of the blade.

20. Lower and basal sheaths possessing a double vestiture of long pilose or villose hairs above shorter pilose or puberulent hairs

21. Plants restricted to hot geothermal soils of the Cascade, Sierra Nevada and Rocky Mnt ranges ..... **Dichanthelium thermale** subsp. **thermale** (in part)
21. Plants not growing in hot geothermal soils ..... **Dichanthelium columbianum** (in part)

20. Lower and basal sheaths possessing a single indument solely of villose hairs

22. Indument of vernal stem sheaths > 2 mm long; spikelets > 1.9 mm long ..... **Dichanthelium villosissimum** (in part)
22. Indument of vernal stem sheaths < 2 mm long; spikelets < 1.9 mm long ..... **Dichanthelium subvillosum**

18. Upper surface of mid-stem leaves of vernal culms lacking pubescence along the central portions of the blade (lacking pubescence along the central one third of the blade from base to tip).

23. Spikelets ≤ 2.1 (rarely to 2.4) mm long; ligule usually > 1.0 mm long; first glume ≤ 1.0 mm long ..... **Dichanthelium columbianum** (in part)
23. Spikelets > 2.1 mm long; ligule usually ≤ 1.0 mm long; first glume typically > 1.0 mm long.

24. Distal sheath of vernal culms possessing a short puberulence (often below longer pilose or villose hairs); ligule of distal vernal stem leaves > 0.7 mm long ..... **Dichanthelium commonsianum** (in part)
24. Distal sheath of vernal culms glabrous, pilose or villose but lacking a short puberulence; ligule of distal vernal stem leaves < 0.7 mm long ..... **Dichanthelium ovale** (in part)

1. **DICHANTHELIUM ACUMINATUM** (Sw.) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1121. 1978. *Panicum acuminatum* Sw., Prodr. 23. 1788. *Panicum dichotomum* var. *acuminatum* (Sw.) Griseb., Fl. Brit. W.I. 553. 1864. **TYPE: JAMAICA**: locality unknown, *Swartz s.n.* (holotype: S; isotypes: BM, US!).

Panicum ciliosum Nash, Bull. Torrey Bot. Club 26: 568. 1899. **TYPE: USA. Mississippi**. Harrison Co.: Biloxi, 1 Sep 1898, *Tracy 4580* (holotype: NY!; isotypes: NCU, US!).

Panicum orangense Ashe, J. Elisha Mitchell Sci. Soc. 15: 113. 1899. **TYPE: USA. North Carolina**. Orange Co.: Chapel Hill, 29 Jun 1898, *Ashe s.n.* (lectotype: US!, designated by Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 220. 1910).

Panicum thurowii Scribn. & J.G. Sm., Circ. Div. Agrostol. USDA 16: 5. 1899. *Dichanthelium acuminatum* var. *thurowii* Gould & Clark, Ann. Missouri Bot. Gard. 65: 1125. 1978. *Panicum acuminatum* var. *thurowii* (Scribn. & J.G. Sm.) Reed, Phytologia 67: 452. 1989. **TYPE: USA. Texas**. Waller Co.: locality unknown, 5 Jun 1898, *Thurow 9* (holotype: US!; isotype: US!).

Panicum auburne Ashe, North Carolina Agric. Res. Serv. Bull. 175: 115. 1900. *Dichanthelium auburne* (Ashe) Mohlenbr., Vasc. Fl. Illinois 419. 2002. **TYPE: USA. Alabama**. Lee Co.: Auburn, 7 May 1898, *Earle & Baker 1527* (holotype: NCU!; isotypes: NY!, US!).

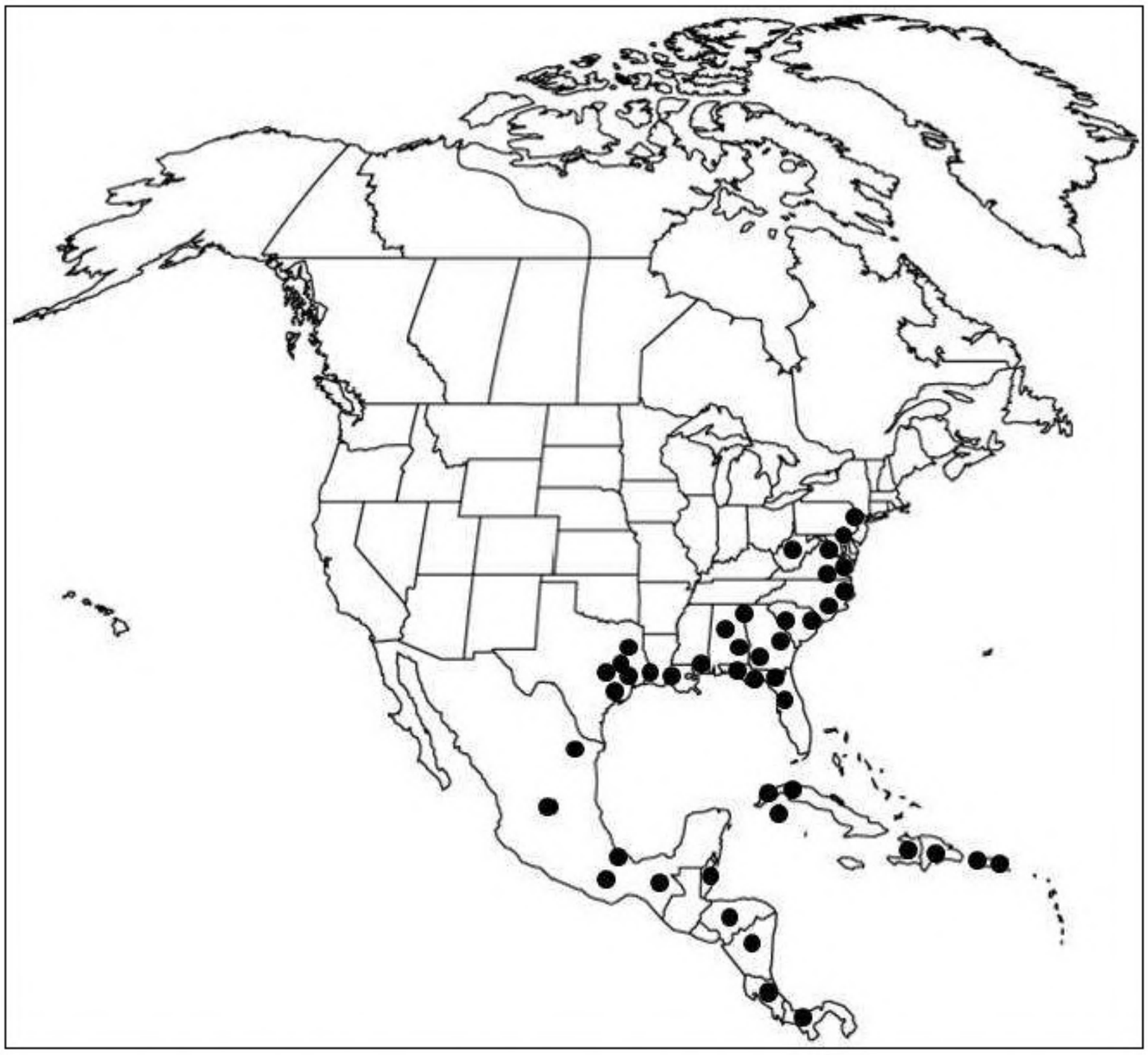
Panicum comophyllum Nash, Bull. Torrey Bot. Club 30: 380. 1903. **TYPE: PUERTO RICO**. San Juan: collected in rich soil at Santurce, 9 Jan 1899, *Heller 12* (holotype: NY!; isotype: fragment US).

Panicum olivaceum Hitchc. & Chase, Contr. U.S. Natl. Herb. 15: 225. 1910. **TYPE: GUATEMALA**. Alta Verapaz: Coban, 1400 m, Feb 1888, *Tuerckheim 428* (holotype: US!; isotypes: ISC!, US!)

Panicum glutinoscabrum Fernald, Rhodora 49:122. 1947. **TYPE: USA. Virginia**. Nansemond Co.: sphagnous and peaty bog by Norfolk and Western Railway, *Fernald, Long, & Clement 15186* (holotype: GH!; isotypes: PH, US!).

Plants erect or ascending from a geniculate base, 20–70 cm tall; lower **internodes** double invested with short, often sparse, pilose hairs below longer villose hairs (Figure 8b, for pubescence type), mid-stem and upper-stem internodes single invested with velutinous or villose hairs (Figure 8a, for pubescence type); **sheaths** conspicuously velutinous to villose (Figure 8a) with hairs 0.2–2.5 mm long, the lower stem sheaths double invested with short, pilose hairs and longer villose hairs (Figure 8b) 0.4–1.3 mm long; **pseudoligule** distinct, 2–4 mm long; **leaf blades** spreading to ascending, 3–12 cm long, 4–13 mm wide, margins ciliate on at least the lower half, adaxial leaf surface glabrate to villous, abaxial surface velutinous; **panicles** 3–11 cm long, half as wide to as wide as long, pilose to

velutinous; **spikelets** 1.6–2.1 mm long, approximately 1 mm wide, elliptic, pilose; **first glume** 0.4–0.9 mm long, typically equal or less than 1/3 the length of the spikelet, acute to broadly acute.



Distribution and habitat. *Dichanthelium acuminatum* is found along the eastern and southern coastal plain of North America, eastern Central America, northern South America, and throughout the Antilles. In North America, it occurs with increasing rarity from coastal regions into the interior. The full extent of its distribution outside of North America is not well documented. Its habitat consists primarily of open woodland and grassland communities with sandy soil.

Representative specimens. BELIZE. Orange Walk District. 25 Jul 1980, *Dwyer & Berry 15016* (MO). **COLOMBIA. Cauca.** 1889, *Lehmann 974* (GH). **COSTA RICA. San Jose.** 26 Dec 1925, *Standley & Valerio 43377* (GH). **DOMINICAN REPUBLIC. Santo Domingo.** 13 Feb 1929, *Ekman 11547* (GH). **GUATEMALA.** Alta Verapaz, Feb 1888, *Turckheim 428* (MO,US). **HAITI.** 28 Sep 1943, *Holdridge 1727* (MO). **HONDURAS. Francisco Morazan.** 23 Oct 1951, *Swallen 11012* (MO). **JAMAICA.** 24 Jan 1913, *Harris 11597* (GH). **MEXICO. Chiapas.** 15 Nov 1984, *Davidse 29845* (MO). **Oaxaca.** 14 Aug 1975, *Davidse & Davidse 9688* (MO). **Tabasco.** 8 Aug 1975, *Davidse 9368* (MO). **Vera Cruz.** 2 Sep 1910, *Hitchcock 134* (MO). Oct 1927, *Purpus 7879* (MO). **NICARAGUA.** Nueva Segovia, 10–13 Aug 1977, *Stevens & Krukoff 3271* (MO). **PANAMA. Chiriqui.** 25 Jun 1938, *Davidson 766* (GH). **USA. Alabama.** Lee Co.: 7 May 1898, *Earle & Baker 1527* (NY). **Florida.** Franklin Co.: *Chapman 7189* (MO). **Georgia.** Burke Co.: 4 Jun 1964, *Freckmann 1180* (MO). **Louisiana.** Acadia Par.: 17 Apr 1913, *Chambliss s.n.* (MO). Jeff Davis Parish, 15 May 1915, *Palmer 7610* (MO). **Mississippi.** Harrison Co.: 1 Sep 1898, *Tracy 4580* (US). **North Carolina.** Orange Co.: 29 Jun 1898, *Ashe s.n.* (US). **Puerto Rico.** 17 Jan 1886, *Hackel 5908* (GH). 9 Jan 1899, *Heller 12* (NY). **Texas.** Montgomery Co.: 11 May 1980, *Morden 29* (MO). Polk

Co.: 10 May 1973, *Gould, Hatch, & Waller 14233A* (MO). Upshur Co.: 28 May 1901, *Reverchon 2355* (MO). Waller Co.: 5 Jun 1898, *Thurow 9* (US). **Virginia**. Nansemond Co.: 2 & 12 Sep 1946, *Fernald, Long, & Clement 15186* (GH).

The treatment of *Dichanthelium acuminatum* presented here is much more restrictive than that of Gould and Clark (1978) and Freckmann and Lelong (2002, 2003) but less so than the treatment of Hitchcock and Chase (1910 and 1950); see discussion for more details. The data demonstrate that *D. acuminatum*, in the present sense, is morphologically distinct from other members of the section in that the stems and leaves are densely pubescence, it has a double ligule consisting of a short true ligule backed by a conspicuous pseudoligule, and, unlike all other members of the section, it has conspicuous marginal cilia that typically extend at least half way up the margins of vernal leaf blades. These marginal hairs have pustulate bases that can be detected even in older specimens that have lost the hairs; abaxial hairs are easily misinterpreted as originating from the margin, so caution and microscopy are recommended. Typically, *D. acuminatum* is the most densely and softly pubescent member of the section and the abaxial blade surfaces of vernal stem leaves are soft to the touch. It also produces an abundance of rosette leaves, which are often proportionately larger than the leaves of other species in the section. This character along with the previously mentioned ciliate leaf margins is reminiscent of members of sect. *Laxiflorae*.

Hitchcock and Chase (1910) maintained the separation of *Panicum olivaceum* and *P. thurowii* from *P. acuminatum* based on plant color. While variation does exist, the abundance of intermediates and the many factors that can influence plant color suggest that this character lacks taxonomic value and consistency. In fact, there appears to be a tendency toward thicker leaves and a more olive-green coloration in many species of grass collected from coastal areas and subtropical regions compared to the same species from interior and temperate regions (personal observ.). Gould and Clark (1978) maintained var. *thurowii* in reference to more robust specimens than typical. While a review of specimens in the present study did suggest some interesting range in morphological variation, the data did not support it as distinct. Similarly, specimens approximating what Hitchcock and Chase (1910) maintained as *P. auburne* demonstrated some intriguing differences in morphology such as a smaller stature, smaller spikelets, and narrower leaves. Also, specimens that could be interpreted as *P. auburne* occurred on the northern fringe of what would otherwise be a narrow circumscription of what is here interpreted as *Dichanthelium acuminatum*. Ultimately, the data analysis strongly supports *D. acuminatum* as a distinct morphological cluster. Subunits of morphological variation within this cluster, though not found to be significant in this study, do maintain the suggestion of cryptic taxa within *D. acuminatum*. Future investigations attempting to more intimately understand these relationships will undoubtedly require extensive field familiarity.

2. DICHANTHELIUM COLUMBIANUM (Scribn.) Freckmann, Phytologia 39: 270. 1978. *Panicum columbianum* Scribn., Bull. Div. Agrostol. USDA 7: 78. 1897. *Panicum acuminatum* var. *columbianum* (Scribn.) Lelong, Brittonia 36: 270: 1984. *Dichanthelium acuminatum* subsp. *columbianum* (Scribn.) Freckmann & Lelong, Sida 20: 167. 2002. **TYPE: USA. District of Columbia**. Brookland, 14 Jul 1894, *Scribner s.n.* (holotype: US!; isotypes: NCU, NY!).

Panicum addisonii Nash, Bull. Torrey Bot. Club 25: 83–84. 1898. *Panicum commonsianum* subsp. *addisonii* (Nash) W. Stone, New Jersey State Mus. Annual Rep. 1910: 205. 1911. *Panicum commonsianum* var. *addisonii* (Nash) Fernald, Rhodora 37: 391. 1935. *Dichanthelium ovale* var. *addisonii* (Nash) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1115. 1978. *Panicum ovale* var. *addisonii* (Nash) C.F. Reed, Phytologia 67: 452. 1989. **TYPE: USA. New Jersey**. Cape May Co.: in sandy soil at Wildwood, 30 & 31 May 1897, *Bicknell s.n.* (holotype: NY!; isotypes: NY!, US).

Panicum scoparioides Ashe, J. Elisha Mitchell Sci. Soc. 15: 53. 1898. *Panicum villosissimum* var. *scoparioides* (Ashe) Fernald, Rhodora 36: 79. 1934. *Dichanthelium scoparioides* (Ashe)

Mohlenbr., Erigenia 6: 26. 1985. **TYPE: USA**. **Delaware**. New Castle Co.: Centerville, dry soil, 25 Jun 1873, *Commons s.n.* (lectotype: US!, designated by Gould & Clark, Ann. Missouri Bot. Gard. 65: 1123. 1978; isotype: NY!).

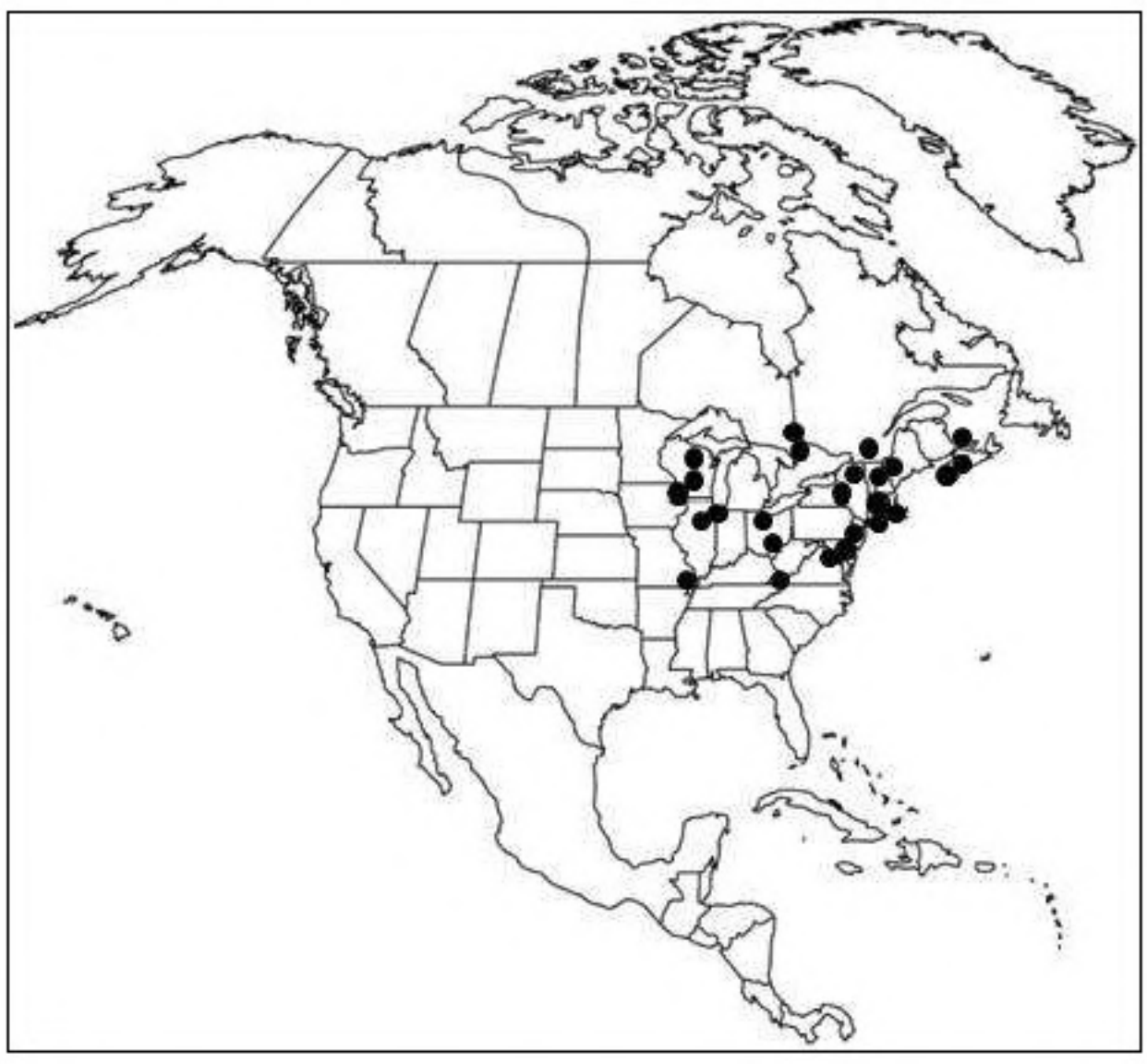
Panicum tsugetorum Nash, Bull. Torrey Bot. Club 25: 86. 1898. **TYPE: USA**. **New York**. Bronx Co.: locality unknown, *Nash 287* (holotype: NY!; isotype: US!).

Panicum lanuginosum var. *siccanum* Hitchc. & Chase, Rhodora 8: 207–208. 1906. *Panicum columbianum* var. *siccanum* (Hitchc. & Chase) Boivin, Le Naturaliste Canadien 95: 526. 1967. **TYPE: USA**. **Illinois**. La Salle Co.: Starved Rock, dry hot sand of sandstone cliff, 13 Jul 1901, *Chase 1602* (holotype: US!).

Panicum unciphyllum var. *thinium* Hitchc. & Chase, Rhodora 8: 209. 1906. *Panicum columbianum* var. *thinium* (Hitchc. & Chase) Hitchc. & Chase, Rhodora 10: 64. 1908. *Panicum heterophyllum* var. *thinium* (Hitchc. & Chase) Hubb, Rhodora 14: 172. 1912. *Dichanthelium sabulorum* var. *thinium* (Hitchc. & Chase) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1113. 1978. **TYPE: USA**. **New Jersey**. Toms River, in mats, sandy open ground, 28 Jul 1906, *Chase 3577* (holotype: US!).

Panicum owenae E.P. Bicknell, Bull. Torrey Bot. Club 35: 185. 1908. **TYPE: USA**. **Massachusetts**. Nantucket Co.: Nantucket, on the sandy commons west of town, 20 Sep 1907, *Bicknell s.n.* (holotype: NY!; isotype: US).

Plants erect or ascending from a geniculate base, 10–50 cm tall; **internodes** and **sheaths** pubescence of short puberulent to pilose hairs and long villose hairs (Figure 8d), occasionally lacking the longer villose hairs on the middle and upper internodes and sheaths (Figure 8c),longer hairs 0.3–2.0 mm long when present; **ligule** 0.9–1.5 mm long; **pseudoligule** sparse, intermeshed, or commonly absent (see Figs. 7b, c or d); **leaf blades** spreading to ascending, 3–9 cm long, 3–8 mm wide, margins ciliate only at the base of blade or eciliate, adaxial leaf surface villose to glabrate, hairs absent along the central third of the blade, abaxial surface with appressed puberulence; **panicles** 2–8 cm long, half as wide to as wide as long, puberulent and often pilose; **spikelets** (1.3–) 1.5–1.9 (–2.2) mm long, approximately 1 mm wide, elliptic, pilose; **first glume** 0.5–1.0 mm long, typically 1/3 to 1/2 as long as the spikelet, obtuse to broadly acute.



Distribution and habitat. *Dichanthelium columbianum* is primarily found in very sandy soils in northeastern North America, the Great Lakes region, and sand prairie and savanna communities in the upper Mississippi watershed. The southernmost collections are from the few remaining sand prairies of southeastern Missouri which are derived from Pleistocene outwash of the Mississippi River. It often becomes a dominant species in sand prairie and dune systems of the upper Midwest where it commonly is found in association with *Lithospermum caroliniense*. The habitats of *D. columbianum* typically consist of dunes, pine woodlands, sand prairies, and open woods with extremely sandy soil profiles.

Representative specimens. **USA**. **Delaware**. New Castle Co.: 25 Jun 1823, *Commons 283* (US). Sussex Co.: 16 Jun 1926, *Fogg Jr. s.n.* (MO). **Illinois**. LaSalle Co.: 13 Jul 1901, *Chase 1602* (US). **Maryland**. Calvert Co.: 8 Jul 1934, *Chase 12270* (MU). **Massachusetts**. Nantucket Co.: 20 Sep 1907, *Bicknell s.n.* (NY). Plymouth Co.: 15 Sep 1916, *St. John 11755* (MU). **New Jersey**. Cape May Co.: 30 May 1897, *Bicknell s.n.* (NY). **New York**. Clinton Co.: 3 Jul 1902, *Eggleston 2843* (MU). Oneida Co.: 3 Jul 1945, *Crockett 7577* (MO). **Ohio**. Hocking Co.: 15 Jun 1982, *Cusick 21692* (MU). Lucas Co.: 19 Jun 1981, *Easterly 12688* (MU).

Dichanthelium columbianum varies widely in degree of pilosity or villosity but consistently possesses a short puberulence on all the internodes and sheaths of the vernal culm. This character, as well as spikelet, first glume, and ligule length are useful in separating it from *D. ovale*. The spikelet lengths of *D. columbianum* can approach those of *D. commonsianum*, in which case the ligule and glume length can be used to separate the two. When a pseudoligule is present in *D. columbianum* it is sparse and weakly differentiated from the true ligule, which can be easily detected with 30x magnification. Plants possessing a pseudoligule are typically more pilose or villose overall than those lacking a pseudoligule. Plants with more dense pilosity or villosity often possess pubescence all across the adaxial leaf surfaces while more sparsely pubescent plants may be nearly glabrous along the adaxial leaf surfaces.

Panicum addisonii is placed into synonymy under *Dichanthelium columbianum*. This is a unique placement, in that previous treatments have never directly associated *P. addisonii* with *D. columbianum*. Rather, it is usually treated under *D. commonsianum* or *D. ovale* evidently on the basis of having spikelets equal to or greater than 2 mm in length (Deam 1940; Fernald 1950; Freckmann & Lelong 2002; Freckmann & Lelong 2003; Gleason & Cronquist 1991; Gould & Clark 1978; Pohl 1947; Radford et al. 1968; Stone 1911). However, the holotype of *P. addisonii* has spikelets that range from 1.8–2.0 mm long which is well within the range of typical *D. columbianum* and outside the range for *D. commonsianum* or *D. ovale*. Furthermore, the length of its ligule and first glume better align it with *D. columbianum*. This confusion is thought to stem from the treatments of Hitchcock and Chase (1910, 1951) wherein the vernal culms of *P. addisonii* are referred to as being "similar to that of *P. commonsianum*." Stone (1911) was the first to subsume *addisonii* under *P. commonsianum*, referring to it as being a diminutive of the typical variety.

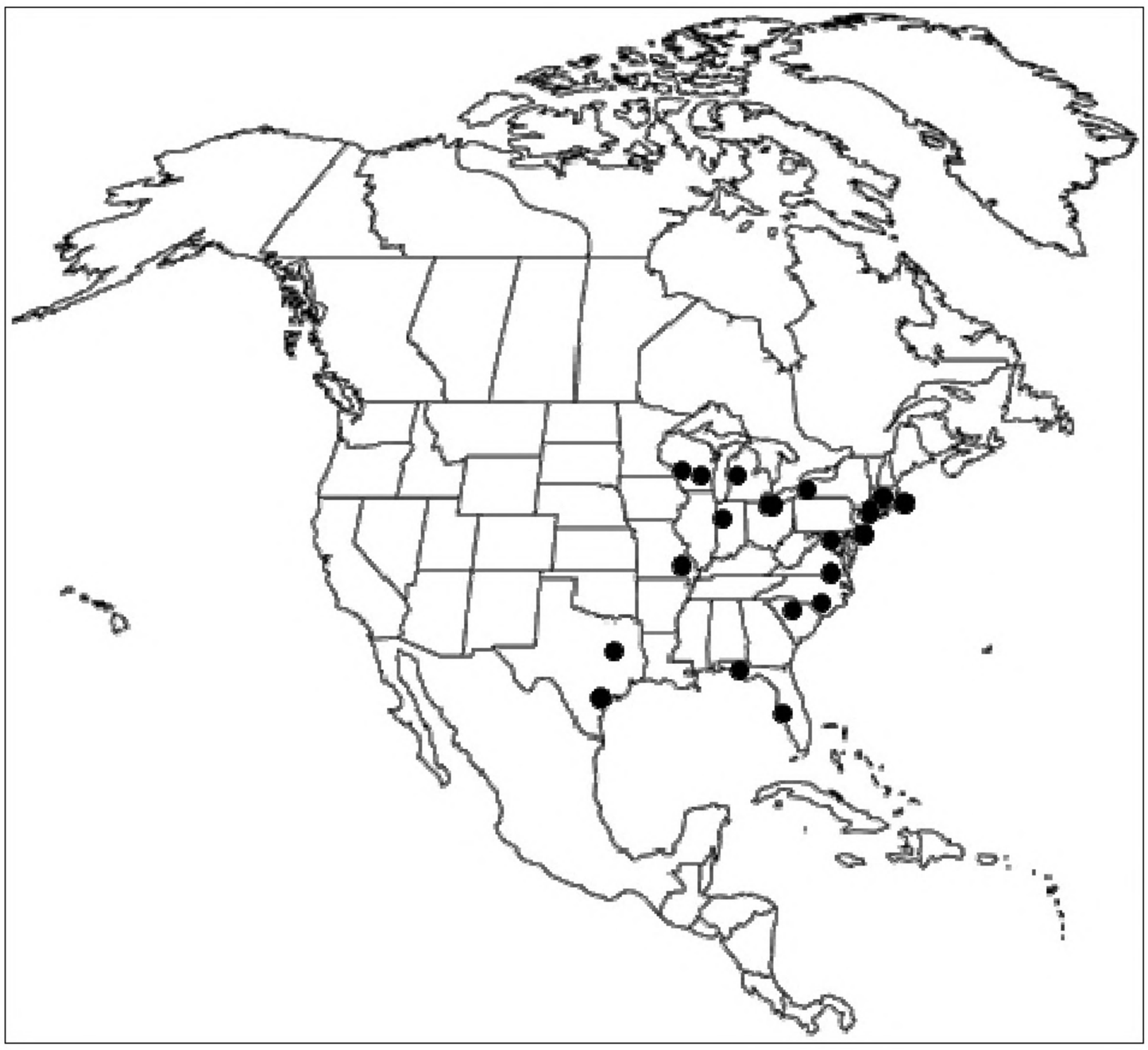
The treatments of Gould and Clark (1978) and Hitchcock and Chase (1910, 1950), included subspecific taxa under *Dichanthelium columbianum*. Hitchcock and Chase (1910, 1950) also maintained *P. tsugetorum* as a similar but separate species. The distinctions in these taxa were based largely on variations in spikelet length and pubescence type. Given the subtly of this variation, its lack of geographical or ecological correspondence and its consistency with levels of variation found in other groups, it is more satisfying to interpret these taxa as being within the range of variation of typical *D. columbianum* rather than maintaining undefinable infraspecific taxa. Extensive field familiarity with *D. columbianum* in the upper Midwest and northeastern North America may uncover some ecological or as yet unnoticed morphological differences worthy of recognition.

3. **DICHANTHELIUM COMMONSIANUM** (Ashe) Freckmann, Phytologia 39: 271. 1978. *Panicum commonsianum* Ashe, J. Elisha Mitchell Sci. Soc. 15: 55. 1898. *Panicum columbianum* var. *commonsianum* (Ashe) Dore, Naturaliste Canad. 103: 562. 1972. **TYPE: USA. New Jersey**. Cape May Co.: Cape May, collected in drifting sands along the coast, 29 Jun 1898, *Commons 341* (holotype: unknown; isotypes: NY!, US!).

Panicum deamii Hitchc. & Chase, Indiana Dept. Cons., Publ. 82: 284. 1929. **TYPE: USA. Indiana**. Lake Co.: collected on crest of low dune a quarter mi S of Pine, 21 Jun 1926, *Deam 43287* (holotype: US!).

Panicum euchlamydeum Shinners, Amer. Midl. Naturalist 32: 170. 1944. *Panicum commonsianum* var. *euchlamydeum* (Shinners) Pohl, Amer. Midl. Naturalist 38: 507. 1947. *Dichanthelium commonsianum* var. *euchlamydeum* (Shinners) Freckmann, Phytologia 39: 271. 1978. **TYPE: USA. Wisconsin**. Adams Co.: sandy slope, PH 7.5, 12 mi SE of Adams, 28 Jun 1942, *Shinners & Shaw 4415* (holotype: WIS!; isotypes: GH, US!).

Plants erect or ascending from a geniculate base, 10–60 cm tall; **internodes** double invested with short puberulent to pilose hairs below a villous pubescence (Figure 8d) or occasionally lacking the longer villous hairs on the middle and upper internodes (Figure 8c); **sheaths** double invested with short puberulent hairs below a pilose or villous pubescence (Figure 8d) or occasionally lacking the longer villous hairs on the middle and upper sheaths (Figure 8c), longer hairs 0.5–3.7 mm long when present; **ligule** 0.5–1.3 mm long; **pseudoligule** sparse or lacking (Figs. 7b or c); **leaf blades** spreading to ascending, 3–11 cm long, 3–7 (–10) mm wide, margins ciliate only at the base of blade or eciliate, adaxial leaf surface glabrate to villous, hairs absent along the longitudinal central third of the blade, abaxial surface with appressed puberulence; **panicles** 3–9 cm long, half as wide to as wide as long, puberulent; **spikelets** 2.2–2.7 mm long, approximately 1 mm wide, elliptic, pilose; **first glume** 0.9–1.8 mm long, typically 2/5 to 1/2 as long as the spikelet, obtuse to broadly acute.



Distribution and habitat. *Dichanthelium commonsianum* is found along the coastal plain of the eastern and southeastern USA from Massachusetts to Texas. Its distribution within the interior of North America is scattered and poorly understood but well-documented from the Great Lakes Region. It is reported from every state east of and including Arkansas, Kansas, and Iowa as well as throughout the Great Lakes region. The present study has verified interior North American collections from Missouri, Wisconsin, Indiana, and Ohio. Where found, *D. commonsianum* is associated with dry sandy soils of open woods, dunes and prairies.

Representative specimens. **USA**. **Delaware**. Sussex Co.: 18 Jun 1905, *Hitchcock 143* (MO). Sussex Co.: 24 Jun 1942, *McVaugh 6512* (MO). **Indiana**. Jasper Co.: 15 Jun 1947, *Friesner 21490* (MO). **Maryland**. Prince George's Co.: 25 Jul 1907, *Chase 146* (MO). **Massachusetts**. Barnstable Co.: 23 Jun 1918, *Fernald 16118* (MO). Barnstable Co.: 4 Aug 1918, *Fernald 16119* (MO). Dukes Co.: 5 Sep 1928, *Fogg Jr. 3875* (MO). **Missouri**. Scott Co.: 7 Sep 1993, *McKenzie 1294* (MO). **New Jersey**. Cape May Co.: 29 Jun 1899, *Commons 341* (US). Mercer Co.: 18 Aug 1866, *E.D. s.n.* (MO). Middlesex Co.: 9 Jul 1905, *MacKenzie 1485* (MO). Ocean Co.: 28 Jul 1907, *MacKenzie 2779* (MO). **New York**. Suffolk Co.: 19 Jul 1927, *Latham 4169* (MO). Suffolk Co.: 4 Aug 1956, *Van Schaak 3550* (MO). Suffolk Co.: 4 Aug 1956, *Van Schaak 3551* (MO). **Texas**. Robertson Co.: 30 Apr 1951, *Launchbaugh 397* (MO). **Wisconsin**. Adams Co.: 28 Jun 1942, *Shinners & Shaw 4415* (UW). La Crosse Co.: 18 Jun 1925, *Pammel 1334* (MO).

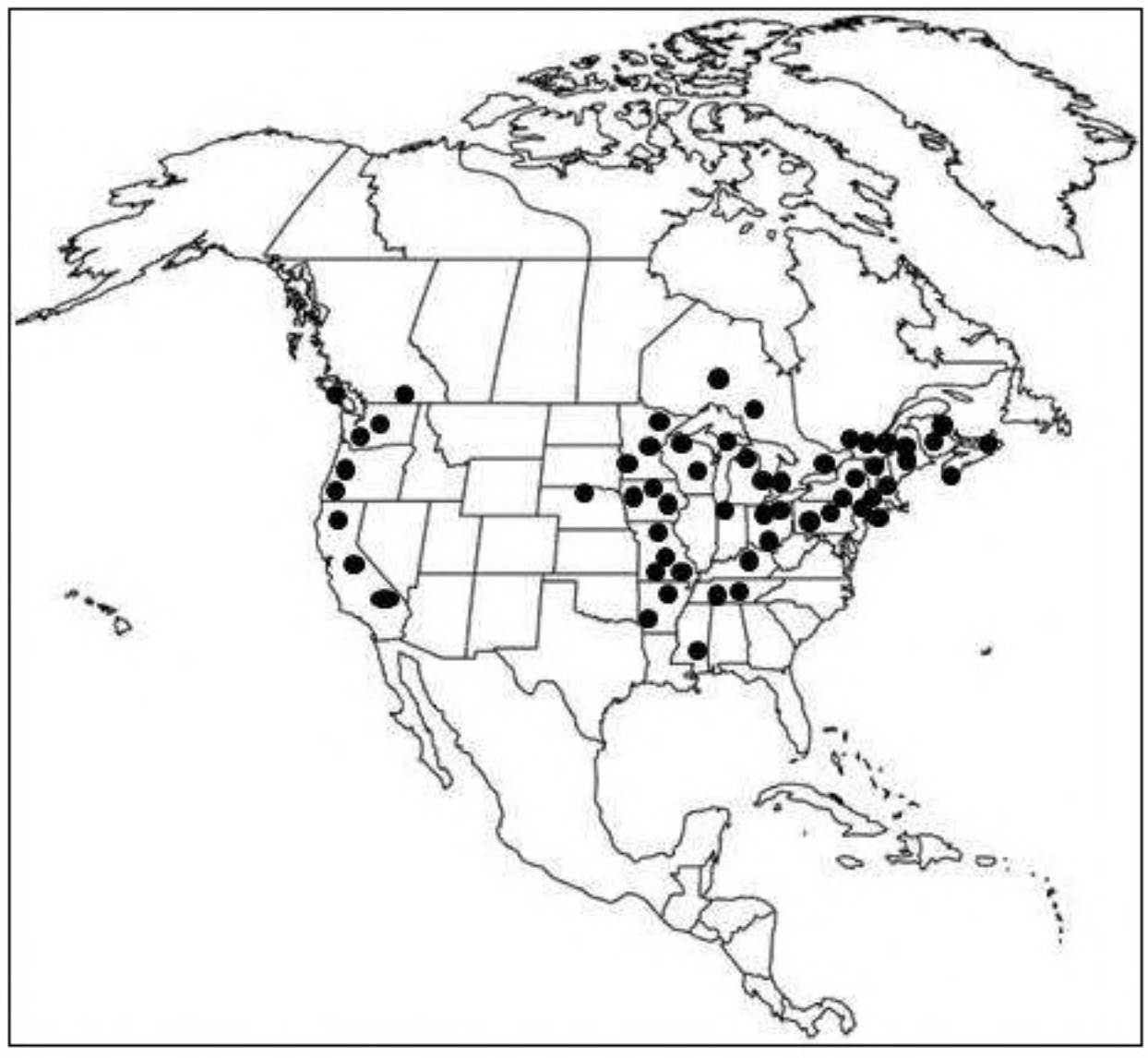
Dichanthelium commonsianum is most similar in morphology to *D. columbianum* and *D. ovale*. It can be distinguished from *D. columbianum* by its larger spikelets, shorter ligule, and longer first glume. It differs from *D. ovale* by the presence of puberulence on internodes and sheaths of the middle and upper culm which *D. ovale* lacks, as well as a longer ligule. There is also a strong tendency for the first glume of *D. commonsianum* to be slightly greater than half the overall spikelet length while the first glume of *D. ovale* is typically less than half the spikelet length. Some authors have included *P. addisonii* as synonymous or infra specific to *D. commonsianum*. For a discussion of this see notes under *D. columbianum*. *Panicum euchlamydeum* and *P. commonsianum* var. *euchlamydeum* are names once used in reference to Midwestern specimens of *D. commonsianum*. However, as is explained in Pohl's (1947) designation to variety, there is little value in maintaining var. *euchlamydeum* other than as representing the inland populations and there does not appear to be any morphological distinction other than a tendency for slightly more pubescence in Midwestern specimens. This is very much in line with finding in the present study as well in a general tendency for both *D. commonsianum* and *D. columbianum*.

4. **DICHANTHELIUM IMPLICATUM** (Scribn.) Kerg., Fl. Descript. France, Suppl. 5: 544. 1979. *Panicum implicatum* Scribn., Bull. Div. Agrostol. USDA 11: 43. 1898. *Panicum unciphyllum* var. *implicatum* (Scribn.) Scribn. & Merr., Rhodora 3: 123. 1901. *Panicum lindheimeri* var. *implicatum* (Scribn.) Fernald, Rhodora 23: 228. 1921. [1922]. *Panicum lanuginosum* var. *implicatum* (Scribn.) Fernald, Rhodora 36: 77. 1934. *Dichanthelium acuminatum* var. *implicatum* (Scribn.) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1126. 1978. 1979. *Panicum acuminatum* var. *implicatum* (Scribn.) Beetle, Phytologia 48: 192. 1981. *Dichanthelium acuminatum* subsp. *implicatum* (Scribn.) Freckmann & Lelong, Sida 20: 167. 2002. **TYPE: USA. Maine**. Cumberland Co.: Cape Elizabeth, on salt marshes, 26 Jul 1895, *Scribner s.n.* (holotype: US!; isotype: NY!).

Panicum occidentale Scribn., Ann. Rep. Missouri Bot. Gard. 10: 48. 1899. **TYPE: CANADA. British Columbia**. Nootka Sound, no date, *T. Haenke s.n.* (holotype: PR; isotype: MO!, US!).

Panicum pacificum Hitchc. & Chase, Contr. U.S. Natl. Herb. 15: 229. 1910. **TYPE: USA. California**. Shasta Co.: Castle Crag, one-fourth miles west of hotel, in moist places in woods, 3 Aug 1908, *A.S. Hitchcock 3070* (holotype: US!; isotype: NY!).

Plants erect or ascending from a geniculate base, 15–55 cm tall; **internodes** conspicuously to sparsely pilose to villose (Figure 8a); **sheaths** conspicuously to sparsely pilose to villose (Figure 8a), hairs 0.9–4.9 mm long; **ligule** 2.0–5.0 mm long (Figure 8a); **pseudoligule** lacking or indistinguishable from ligule; **leaf blades** spreading to ascending, 2.0–6.5 (–8) cm long, 2.0–6.0 (–8) mm wide, margins ciliate only at the base of blade or eciliate, adaxial leaf surface villous with the longest hairs often 3.0–6.0 mm long, abaxial surface pilose with the longest hairs often 0.8–2.0 mm long ; **panicles** 3–6 cm long, half as wide to as wide as long, densely to sparsely pilose; **spikelets** 1.3–1.7 mm long, approximately 0.7–1.0 mm wide, elliptic, pilose; **first glume** 0.3–0.7 mm long, typically equal or less than 1/3 the length of the spikelet, acute to broadly acute.



Distribution and habitat. *Dichanthelium implicatum* is found across southern Canada from British Columbia to Nova Scotia. In the USA it is found from Kansas north to Minnesota and east to Tennessee and Maine, plus the states of California, Oregon, and Washington. It is also listed as naturalized in southern Europe (Coste 1979); though this might actually be a misapplication of the name. The habitat of *D. implicatum* is highly variable and includes dry, open habitats with sandy soils such as dunes, sand prairies, and sandy or cherty woods. It is also occasionally found in bogs with acidic soils.

Representative specimens. **CANADA**. **Ontario**. Prince Edward Co.: 10 Jul 1947, *Gillett 1366* (MO). **USA**. **Arkansas**. Fulton Co.: 19 May 1909, *Bush 5637* (MO). **California**. Shasta Co.: 3 Aug 1908, *Hitchcock 3070* (US). **Iowa**. Johnson Co.: *Shimek s.n.* (MO). **Ohio**. Lucas Co.: 1 Jul 1997, *McCormac 5971* (MO). **Oregon**. 1871, *Hall s.n.* (MO). Curry Co.: 11 Jul 1919, *Peck 8795* (MO). **Maine**. Lincoln Co.: 13 Jul 1922, *Grover s.n.* (MO). Cumberland Co.: 25 Jul 1895, *Scribner* (US). **Massachusetts**. Berkshire Co.: 16 Jul 1917, *Churchill s.n.* (MO). Middlesex Co.: 27 Jun 1915, *Forbes s.n.* (MO). **Minnesota**. Anoka Co.: 7 Jul 1926, *Stoltz s.n.* (MO). Anoka Co.: 10 Aug 1926, *Stoltz s.n.* (MO). Chippewa Co.: 9 Jul 1982, *Gereau 1014* (MO). Itasca Co.: 30 Jun 1935, *Rosendahl & Maple 707* (MO). **New York**. Tompkins Co.: 18 Jul 1917, *Wiegand, Bechtel & Gershoy 7504*

(MO). **Rhode Island**. Providence Co.: *Olney s.n.* (MO). **Tennessee**. Coffee Co.: 20 Jun 1938, *Svenson 9230* (MO). **Vermont**. Caledonia Co.: *Seymour 18632* (MO). **Washington**. *Presl 3978* (MO). Chelan Co.: 25 Jun 1931, *Thompson 6928* (MO). **Wisconsin**. Bayfield Co.: 10 Jul 1938, *Fassett, Curtiss & Knowlton 19571* (MO).

The morphologies expressed by *Dichanthelium implicatum* and *D. lanuginosum* can be superficially similar. This is especially true when dealing with small *D. lanuginosum* and large *D. implicatum*. However, the vast majority of specimens of both species are distinct. *Dichanthelium implicatum* inhabits a much narrower ecological niche and is significantly more conservative than *D. lanuginosum*. Compared to *D. lanuginosum*, it is smaller in stature and the larger vernal leaves are less than 7.0 cm long. The longer hairs on the adaxial surface of vernal leaves average 3.2 mm in *D. implicatum* compared to 2.3 mm in *D. lanuginosum*. The longer hairs of the abaxial surface of vernal leaves average 0.9 mm long in *D. implicatum*, while in *D. lanuginosum* they average 0.6 mm. Furthermore, upon drying naturally the vernal leaves of *D. implicatum* often become strongly reflexed.

The similarities of the two species have prompted several authors (Braun 1967; Gleason & Cronquist 1991; Fernald 1950; Radford et al. 1968; Scoggan 1978; Steyermark 1963) to treat *Dichanthelium implicatum* as a variety of *D. lanuginosum*. Pohl (1947), in his treatment of Pennsylvania's grasses, followed the treatment of Hitchcock and Chase (1910) in which *P. lanuginosum* (often representing the nomenclatural misapplication of what is here treated as *D. acuminatum*) was restricted to the southeastern coastal plain. He then applied the name *P. implicatum* to what is here treated as *D. lanuginosum*. This treatment has since found its way into several floras in the Great Lakes Region (Swink & Wilhelm 1994; Voss 1972; Voss & Reznicek 2012) and no doubt added to the confusion of species concepts. It is also worth noting that *D. implicatum* is limited to the northern half of the geographical range of *D. lanuginosum*.

The type specimens of two species, *Panicum pacificum* and *P. occidentale*, described from western North America, are here treated as synonymous with *D. implicatum*. However, there are notable differences in these western populations, including wider leaves and differences in pubescence density that warrant further investigation. Many "non-type" specimens labeled "*P. pacificum*" and "*P. occidentale*" clearly belong to *D. lanuginosum* rather than *D. implicatum*. This is most likely due to erroneous identification rather than actual taxonomic confusion. *Dichanthelium implicatum* can superficially resemble *D. meridionale* but differs in its lack of a double vestiture (or at least no puberulence below the villose and pilose pubescence).

5. DICHANTHELIUM LANUGINOSUM (Ell.) Gould, *Brittonia* 26: 60. 1974. *Panicum lanuginosum* Ell., Sketch Bot. S. Carolina 1: 123. 1816. *Panicum dichotomum* var. *lanuginosum* (Ell.) Wood, Class-book of Botany 786. 1861. **TYPE: USA. Georgia**. unknown locality, unknown date, *Baldwin s.n.* (holotype: CHARL; fragment and photo, US!).

Panicum dichotomum var. *fasciculatum* Torr., Fl. N. Middle U.S. 145. 1824. *Panicum huachucae* var. *fasciculatum* (Torr.) F.T. Hubb., Rhodora 14: 171. 1912. *Panicum lindheimeri* var. *fasciculatum* (Torr.) Fernald, Rhodora 23: 228. 1921 [1922]. *Panicum lanuginosum* var. *fasciculatum* (Torr.) Fernald, Rhodora 36: 77. 1934. *Dichanthelium lanuginosum* var. *fasciculatum* (Torr.) Spellenb., Madrono 23: 145. 1975. *Dichanthelium acuminatum* var. *fasciculatum* (Torr.) Freckmann, Phytologia 48: 108. 1981. *Panicum acuminatum* var. *fasciculatum* (Torr.) Beetle, Phytologia 49: 40. 1981. *Dichanthelium acuminatum* subsp. *fasciculatum* (Torr.) Freckmann & Lelong, Sida 20: 167. 2002. **TYPE: USA. New Jersey**. unknown locality, in sandy fields, unknown date, *Torrey s.n.* (holotype: NY).

Panicum huachucae Ashe, J. Elisha Mitchell Sci. Soc. 15: 51. 1898. *Panicum lanuginosum* var. *huachucae* (Ashe) Hitchc., Rhodora 8: 208. 1906. **TYPE: USA. Arizona**. Huachuca Mountains, 1882, *Lemmon s.n.* (lectotype: US!, designated by Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 214. 1910).

Panicum tennesseense Ashe, J. Elisha Mitchell Sci. Soc. 15: 52. 1898. *Panicum lindheimeri* var. *tennesseense* (Ashe) Farw., Amer. Midl. Naturalist 11: 45. 1928. *Panicum lanuginosum* var. *tennesseense* (Ashe) Gleason, Phytologia 4: 21. 1952. **TYPE: USA. Tennessee**. La Vergne Co.: cedar glades, 7 Aug 1897, *Biltmore 7087* (holotype: location unknown; isotypes: NY!, US!).

Panicum nitidum var. *pilosum* Torr., Fl. N. Middle U.S. 146. 1824. *Panicum lindheimeri* subvar. *pilosum* (Torr.) Farw., Amer. Midl. Naturalist 11: 45. 1928. *Panicum lanuginosum* subvar. *pilosum* (Torr.) Farw., Pap. Michigan Acad. Sci. 26: 5. 1941. **TYPE: USA. New York**. unknown locality, in dry woods & c. New York, no date, unknown collector (holotype: NY?).

Panicum nitidum var. *ciliatum* Torr., Fl. N. Middle U.S. 146. 1824. **TYPE: USA. New Jersey**. unknown locality, no date, unknown collector (holotype: NY?).

Panicum funstonii Scribn. & Merr., Circ. Div. Agrostol. USDA 35: 4. 1901. **TYPE: USA. California**. Tulare Co.: collected on the bank of the Kaweak River at Three Rivers, 26 Jul 1891, *Coville & Funston 1286* (holotype: US!).

Panicum unciphyllum f. *prostratum* Scribn. & Merr., Rhodora 3: 124. 1901. **TYPE: USA. Maine**. York Co.: unknown locality, 26 Sep 1897, *Fernald s.n.* (holotype: US!).

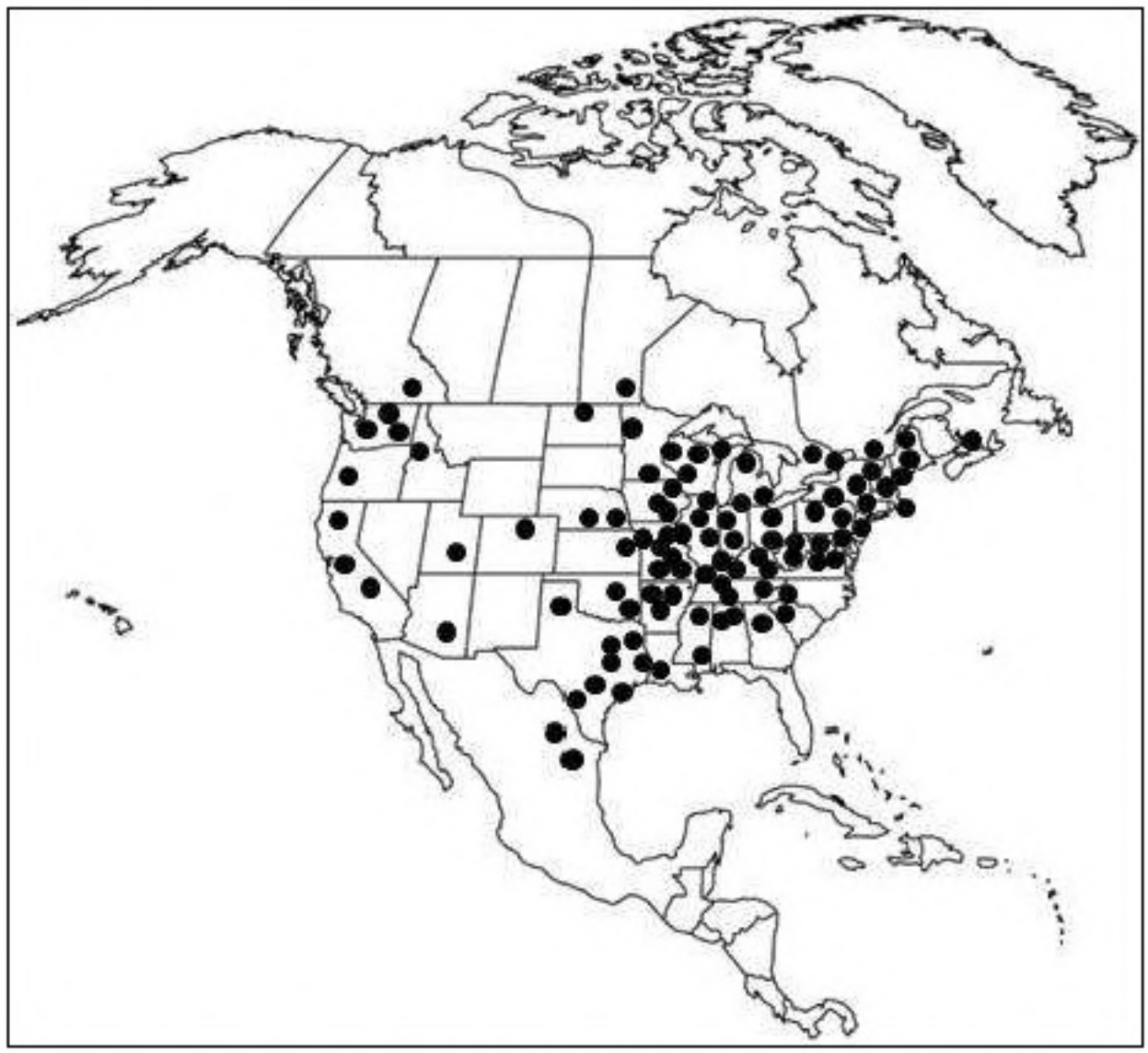
Panicum huachucae var. *silvicola* Hitchc. & Chase, Rhodora 10: 64–65. 1908. **TYPE: USA. District of Columbia**. Reno, 28 Jun 1904, *Chase 2400* (holotype: US!).

Panicum lindheimeri var. *septentrionale* Fernald, Rhodora 23: 227–228. 1921 [1922]. *Panicum lanuginosum* var. *septentrionale* (Fernald) Fernald, Rhodora 36: 77. 1934. *Dichanthelium acuminatum* var. *septentrionale* (Fernald) Mohlenbr., Ill. Fl. Illinois (ed. 2) Grasses: *Panicum* to *Danthonia*: 383. 2001. **TYPE: CANADA. New Brunswick**. Woodstock, river gravels and shingly border of thicket by the St. John River, 14 Jul 1916, *Fernald & Long 12527* (holotype: GH!).

Panicum brodiei H. St. John, Fl. SE Washington 51. 1937. **TYPE: USA. Washington**. Wawawai, Snake River, 1898, *Brodie s.n.* (holotype: WS!; isotype: US).

Plants erect or ascending from a geniculate base, 15–75 cm tall; **internodes** conspicuously to sparsely pilose to villose (occasionally velutinose) (Figure 8a); **sheaths** copiously to sparsely pilose to villose (Figure 8a), hairs (0.7–) 1.2–2.5 (–3.9) mm long, sheath margins ciliate; **ligule** (2.0–) 2.4–4.3 (–5.0) mm long (Figure 8a); **pseudoligule** lacking or indistinguishable from ligule; **leaf blades** spreading to ascending, 3–12 cm long, 3–12 mm wide, margins ciliate only at the base of blade or eciliate, adaxial leaf surface glabrate to villous with the longest hairs typically 1.3–3.0 mm long, abaxial surface short pilose with the longest hairs typically 0.1–0.7 mm long; **panicles** 3–12 cm long, half as wide to as wide as long, densely to sparsely pilose; **spikelets** 1.3–1.9 mm long, approximately 0.7–1.1 mm wide, elliptic, pilose; **first glume** 0.3–0.7 mm long, typically equal or less than 1/3 the length of the spikelet, acute to broadly acute.

Distribution and habitat. *Dichanthelium lanuginosum* is found throughout North America but is most common in the central and eastern USA. Being the most generalist species within the section, *D. lanuginosum* inhabits a wide range of habitat types and is by far the most frequently encountered taxon in the section. It is most commonly associated with dry open habitats such as prairies, open woods, old fields, and forest edges.



Representative specimens. **CANADA**. **British Columbia**. Nelson Co.: 20 Jul 1939, *Thompson 14433* (MO). Vancouver Island, 26 Jun 1907, *Rosendahl 1931* (MO). **Ontario**. Pipineau Co.: 19 Jul 1947, *Dore 1051* (MO). **Quebec**. Missisquoi Co.: 10 Aug 1923, *Knowlton s.n.* (MO). **USA**. **Arkansas**. Benton Co.: 18 Jun 2002, *Thomas 1502* (private). **Arizona**. Mt. Huachuca, 1882, *Lemmon 2907* (US). **California**. Shasta Co.: 3 Aug 1908, *Hitchcock 136* (MO). Tulare Co.: 26 Jul 1891, *Coville & Funston 1286* (US). **District of Columbia**, 28 Jun 1904, *Chase 2400* (US). **Illinois**. Macon Co.: 12 Jun 1915, *Clokey 2440* (MO). Morgan Co.: 16 Jun 1999, *Hill 31708* (MO). Tazewell Co.: 23 Jun 1919, *Chase 3146* (MO). **Indiana**. Morgan Co.: 11 Jun 1934, *Friesner 7497* (MO). **Iowa**. Wapello Co.: 23 Jun 1939, *Hayden 925* (MO). **Kansas**. Douglas Co.: 15 Jun 1992, *McGregor 40533* (MO). **Kentucky**. Ballard Co.: 2 Jun 1923, *Anderson s.n.* (MO). **Louisiana**. Lake Charles Par.: 21 Apr 1906, *Hitchcock 1147* (MO). **Maine**. York Co.: 26 Sep 1897, *Fernald s.n.* (US). **Maryland**. Balto Co.: 21 Jun 1940, *Reed 2165* (MO). **Massachusetts**. Bristol Co.: 28 Jun 1961, *Seymour 19272* (MO). **Missouri**. Jasper Co.: 2 Jun 1912, *Palmer 3714* (MO). Jasper Co.: 9 Jun 1912, *Palmer 3753* (MO). **Nebraska**. Kearney Co.: 8 Jul 1918, *Hapeman s.n.* (MO). Nemaha Co.: 22 Jun 1972, *Churchill 200* (MO). **New Jersey**. Hunterdon Co.: 12 Jul 1915, *Fisher s.n.* (MO). **New York**. Tompkins Co.: 12 Jul 1913, *James 88* (MO). **Ohio**. Huron Co.: 20 Jun 1887, *Leonard 14* (MO). Scioto Co.: 27 Jun 1934, *Demaree 10756* (MO). **Oklahoma**. Creek Co.: 11 Jun 1939, *Harvey 808* (MO). LeFlore Co.: 17 May 1936, *Demaree 12712* (MO). **Oregon**. Lane Co.: 14 Jun 1928, *Peck 15950* (MO). **Pennsylvania**. Montgomery Co.: 15 Jun 1899, *MacElwee 544* (MO). Philadelphia Co.: no date, *Bigyn s.n.* (MO). **South Carolina**. Anderson Co.: May 1924, *Davis s.n.* (MO). **Texas**. Wheeler Co.: 25 Jun 1957, *Correll & Johnston 17045* (MO). **Utah**. San Juan Co.: 2 Jul 1933, *Maguire 5910* (MO). **Virginia**. Augusta Co.: 5 Jul 1937, *Allard 3170* (MO). **Washington**. Kittilas Co.: July 1898, *Sandberg & Leiberg 425* (MO). Okanogan Co.: Jul 1897, *Elmer 489* (MO). Whitman Co.: Jun 1898, *Brodie s.n.* (WS). **Wisconsin**. La Crosse Co.: 8 Jul 1975, *Ziegler 1656* (MO).

Dichanthelium lanuginosum exhibits considerable morphological variation across its range and in different habitats. In western North America the spikelets typically range from 1.7–1.9 mm long. In deeply shaded environments plants are more sparsely pubescent, the stems often become diffusely branched and the plants tend to sprawl. Also, the leaves often become thinner, wider, and darker green and the inflorescences are smaller and fewer-flowered. In dry habitats with high light the plants are smaller, more stiffly pubescent, more erect, and produce larger inflorescences with many spikelets. It is these latter specimens that most closely approach *D. implicatum* (see notes under *D. implicatum*). In moist, well-drained habitats plants are often sparsely pubescent on the sheaths and lack pubescence on the adaxial leaf surfaces. These plants have previously been called *P. tennesseense*, *P. lanuginosum* var. *tennesseense*, and *P. lanuginosum* var. *septentrionale*. However, given that the spectrum of pubescence is so closely associated with light and moisture, there seems to be little justification for any taxonomic recognition (see notes under *D. lindheimeri*).

Much of the taxonomic confusion surrounding *Dichanthelium lanuginosum* began with the regional misapplication of the name and its association with *D. acuminatum* (see discussion). Lelong (1984) claimed that the type specimens of *P. acuminatum* and *P. lanuginosum* are identical. However, the present study found several meaningful morphological differences between these types. The long, clearly single ligule and the absence of extensive marginal cilia on the leaf blades of *D. lanuginosum* easily distinguish it from *D. acuminatum* which has a short ligule (backed by a longer pseudoligule) and conspicuous marginal cilia along the leaf blades. While the geographical ranges of these two species do overlap along the coastal plain, *D. acuminatum* does not typically occur in the interior of North America.

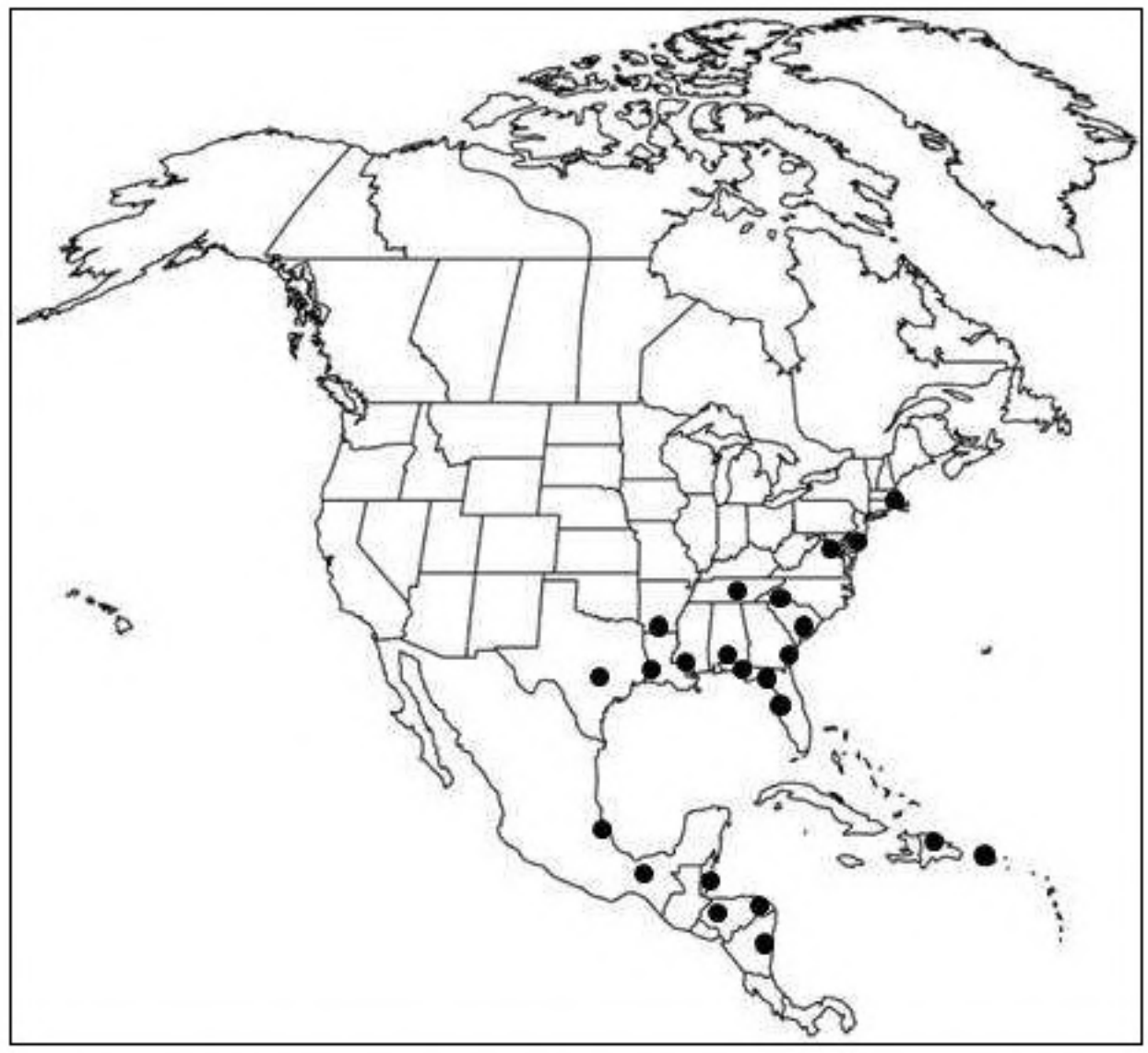
As the paragon of morphological and ecological plasticity, *Dichanthelium lanuginosum* is undoubtedly responsible for the majority of the confusion within sect. *Lanuginosa*. Having carefully observed this plasticity in the field for over a decade and a half, it appears to originate from highly involved breeding systems which may consist of varying combinations of selfing, outcrossing, and population level introgression with other seeming random members of the genus, often with little fidelity to other members of its own section. While the polymorphic nature of this species will confuse, humiliate, confound, and intimidate those unfamiliar with the degrees and directions of morphological expression to which it is capable of rising, given ample field experience its range of variability is certainly intelligible; though it takes more patience than most are willing to grant. As the requisite familiarity is acquired, one begins to pick up on patterns like the tendency of pubescence density and spikelet length to correlate to habitat wetness and acidity, as well as the situational reliability of the more variable character states. One thing is certain, *D. lanuginosum*, like many members of the section and even the genus, cannot be resolved in the mind of the taxonomist without extensive personal familiarity and a willingness to release it from the preconceived patterns and relationships one expects from less complicated groups.

6. **DICHANTHELIUM LEUCOTHRIX** (Nash) Freckmann, Phytologia 48: 101. 1981. *Panicum leucothrix* Nash, Bull. Torrey Bot. Club 24: 41. 1897. *Panicum acuminatum* var. *leucothrix* (Nash) Lelong, Brittonia 36: 271. 1984. *Dichanthelium acuminatum* subsp. *leucothrix* (Nash) Freckmann & Lelong, SIDA 20: 167. 2002. **TYPE: USA. Florida.** Lake Co.: low pine land at Eustis, 16–31 Jul 1894, *Nash 1338* (holotype: NY!; isotypes: MO!, NCU, US).

Panicum parvispiculum Nash, Bull. Torrey Bot. Club 24: 347. 1897. **TYPE: USA. Georgia.** McIntosh Co.: collected at Darien Junction, 25–27 Jun 1895, *Small s.n.* (holotype: NY!; isotype: NY!, US).

Plants erect or ascending from a geniculate base, 10–50 cm tall; **internodes** short puberulent, occasionally also sparsely pilose on lower culms (Figs. 7c or d); **sheaths** puberulent, occasionally also pilose (Figs. 7c or d), longer hairs 0.3–1.6 mm long when present; **ligule** 2.2–4.0 mm long

(Figure 8a); **pseudoligule** absent or indistinguishable from ligule; **leaf blades** spreading to ascending, 2–7 cm long, 2.0–5.0 (–7.0) mm wide, margins ciliate only at the base of blade or eciliate, adaxial leaf surface puberulent to glabrate, abaxial surface puberulent; **panicles** 3–8 cm long, half as wide to as wide as long, puberulent and often pilose; **spikelets** 1.2–1.5 mm long, approximately 0.5–0.8 mm wide, elliptic, puberulent to pilose; **first glume** 0.3–0.5 mm long, typically 1/3 as long as the spikelet, obtuse to acute.



Distribution and habitat. *Dichanthelium leucothrix* is found along the coastal plain of North America from New Jersey to eastern Mexico and inland to Tennessee. It also occurs in Central America, northern South America, and the Caribbean. The habitat of *D. leucothrix* consists of wet to moist, often sandy, woodlands, pine savannas, and bogs.

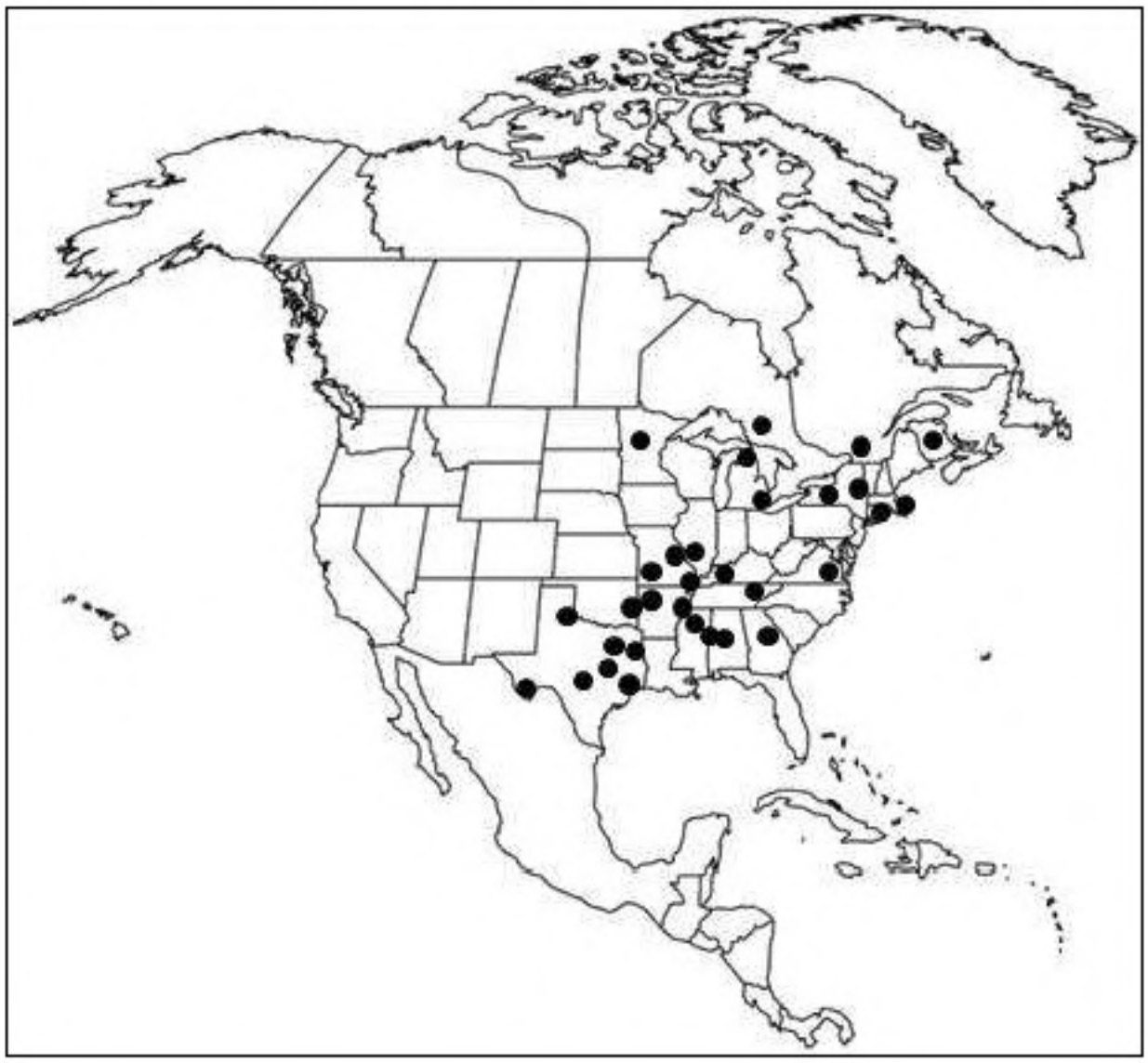
Representative specimens. **USA**. **Florida**. Fauquier Co.: 26 May 1903, *Tracy 8410* (MO). Hillsborough Co.: 2 Apr 1927, *O'Neill 2513* (MO). Lake Co.: 16–31 Jul 1894, *Nash 1338* (NY). **Georgia**. McIntosh Co.: 25–27 Jun 1895, *Small s.n.* (NY). **South Carolina**. Orangeburg Co.: 19 Aug 1905, *Hitchcock 118* (MO). **Tennessee**. Coffee Co.: 20 Jun 1938, *Svenson 9225* (MO). **Texas**. Robertson Co.: 30 Apr 1951, *Launchbaugh 394* (MO).

Dichanthelium leucothrix is one of the smaller members of the section and is similar to *D. wrightianum*, *D. longiligulatum*, and *D. meridionale* in leaf dimensions, presence of puberulence, and ligule length. This group is so distinct that it would not be difficult to justify them as a distinct section. Gould and Clark (1978) treated both *D. longiligulatum* and *D. wrightianum* as varieties of *D. acuminatum* and lumped *D. leucothrix* and *D. meridionale* with *D. acuminatum* var. *implicatum* (*D. implicatum* in present treatment). Given the absence of puberulence on the culms in *D. implicatum* and its larger spikelets, among other characters, Gould and Clark's lumping is not morphologically justified by the present study. Lelong (1984) and Freckmann and Lelong (2002, 2003) designated *D. leucothrix* as a subspecies of *D. acuminatum* (or *P. acuminatum*). Zuloaga et al. (1993b) placed *D. leucothrix* into synonymy under *P. acuminatum* var. *longiligulatum*. Compared to *D. acuminatum*, *D. leucothrix* has a distinctly different ligule (longer and lacking pseudoligule versus short ligule backed

by pseudoligule in *D. acuminatum*), does not possess extensive marginal cilia on vernal leaves, is much smaller in stature, has a close puberulence that *D. acuminatum* lacks, and has much smaller spikelets (averaging 1.3 mm versus 1.8 mm). *Dichanthelium leucothrix* differs from *D. longiligulatum* in possessing conspicuous pubescence on the sheaths and adaxial leaf surfaces of vernal culms.

7. **DICHANTHELIUM LINDHEIMERI** (Nash) Gould, Brittonia 26: 60. 1974. *Panicum lindheimeri* Nash, Bull. Torrey Bot. Club 24: 196. 1897. *Dichanthelium acuminatum* var. *lindheimeri* (Nash) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1127. 1978. *Panicum lanuginosum* var. *lindheimeri* (Nash) Fernald, Rhodora 36: 77. 1934. *Dichanthelium lanuginosum* var. *lindheimeri* (Nash) Harvill, Castanea 42: 177. 1977. *Panicum acuminatum* var. *lindheimeri* (Nash) Beetle, Phytologia 48: 193. 1981. *Dichanthelium acuminatum* subsp. *lindheimeri* (Nash) Freckmann & Lelong, Sida 20: 168. 2002. **TYPE: USA. Texas**. Comal Co.: springs, banks of Guadeloupe, near New Braunfels, May 1946, *Lindheimer 565* (holotype: NY! isotypes: MO!, NY!, US!).

Plants erect or ascending from a geniculate base, 15–100 cm tall; **internodes** glabrous to sparsely pilose; **sheaths** glabrous or lowermost sparsely pilose, margins ciliate; **ligule** 2.0–3.2 mm long (Figure 8a); **pseudoligule** absent; **leaf blades** spreading to ascending, 3–10 cm long, 3–12 mm wide, margins ciliate at the base of blade or eciliate, adaxial leaf surface glabrous to glabrate, abaxial surface glabrous; **panicles** 3–12 cm long, half as wide to as wide as long, glabrous to sparsely pilose; **spikelets** 1.3–1.7 mm long, approximately 0.7–1.0 mm wide, elliptic, pilose; **first glume** 0.3–0.6 mm long, typically equal or less than 1/3 the length of the spikelet, acute to broadly acute.



Distribution and habitat. *Dichanthelium lindheimeri* is found throughout central and eastern North America as well as California, Oregon, and New Mexico. In its southern range and in the Great Lakes region, *D. lindheimeri* is most commonly associated with sandy, ephemerally wet soils. In the central and northern regions of its range it is more commonly associated with floodplains, stream sides, and lake shores.

Representative specimens. **CANADA**. **New Brunswick**. Carleton Co.: 14 Jul 1910, *Fernald & Long 12527* (GH). **USA**. **Arkansas**. St. Francis Co.: 19 Jun 1956, *McDaniel 568* (MO). **Kentucky**. Caldwell Co.: 27 May 1970, *Conrad 1008* (MO). **Michigan**. Emmet Co.: 28 Jul 1922, *Gates 13354* (MU). Washtenaw Co.: 5 Jul 1935, *Hermann 6839* (MO). **Missouri**. Carter Co.: 16 May 2001, *Thomas 1416* (private). Howell Co.: 5 Jun 1999, *Thomas 678* (private). **New York**. Albany Co.: 23 Jun 1951, *Van Schaak 3230* (MO). Cayuga Co.: 25 Jul 1916, *Metcalf 5539* (MO). **Texas**. *Lindheimer 5651846* (NY). Gregg Co.: 18 Jun 1901, *Reverchon 2357* (MO).

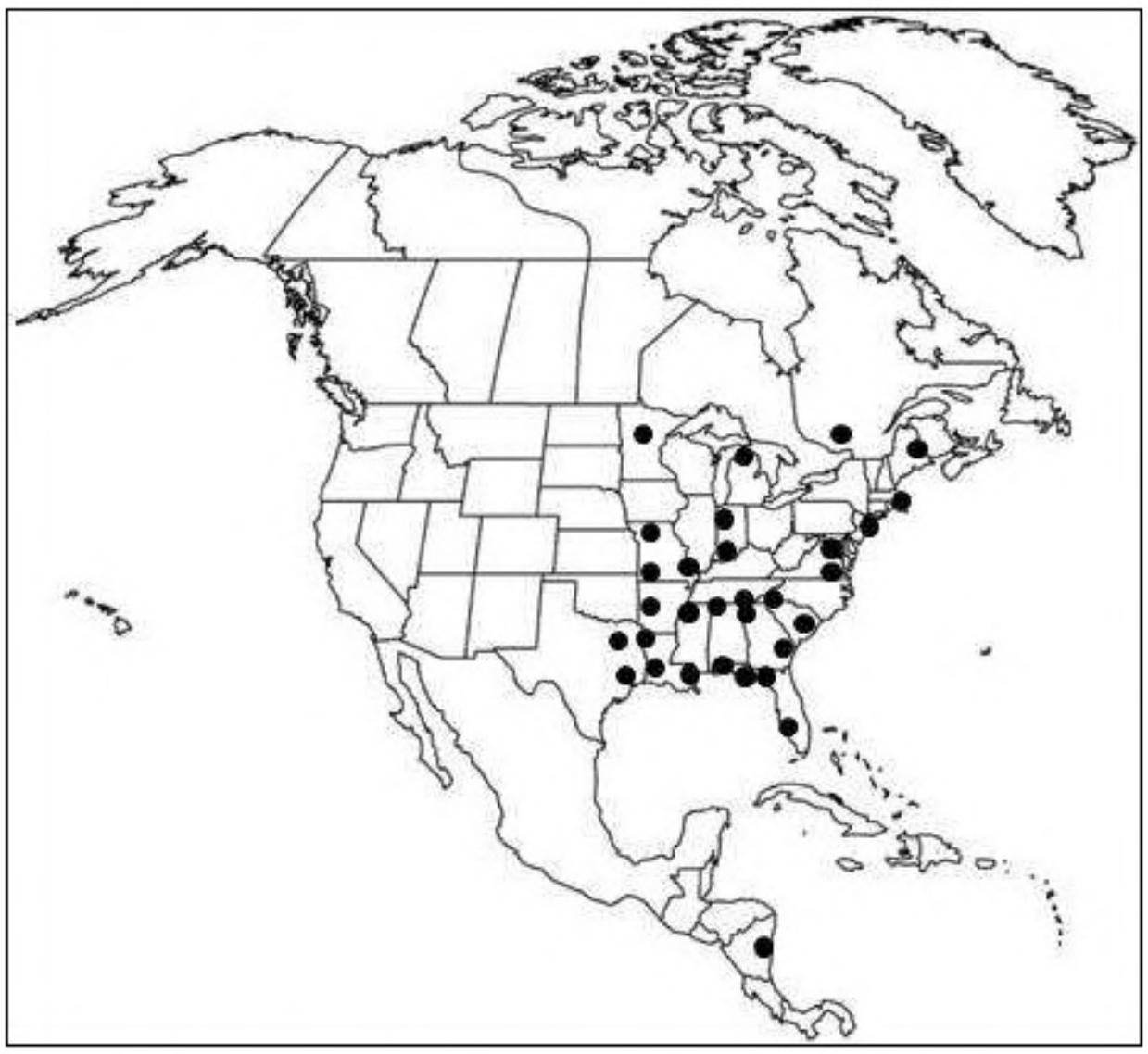
Superficially, *Dichanthelium lindheimeri* appears to be a glabrous variety or even a form of *D. lanuginosum*. In fact, many authors (Braun 1967; Gleason & Cronquist 1991; Fernald 1950; Radford et al. 1968; Scoggan 1978; Steyermark 1963) have placed it in this context. However, *D. lindheimeri* differs significantly from *D. lanuginosum* in several characters. The middle and upper internodes and sheaths of the vernal culms, the adaxial leaf surfaces (except for marginal cilia), and the central axis of the inflorescences are glabrous versus densely to sparsely pilose in *D. lanuginosum*. The margins at the base of vernal stem leaves in *D. lindheimeri* possess long hairs that are thin and crooked versus hairs that are rigid and straight in *D. lanuginosum*. The ligule of *D. lindheimeri* averages 2.4 mm long versus 3.1 mm long in *D. lanuginosum*. Although some overlap does occur, t-test for ligule length between these two species demonstrated a significant difference ($P<0.005$). Fourth, the typical habitats of *D. lindheimeri* are much wetter than *D. lanuginosum* and include stream and lake margins, sandy coastal marshes, and floodplains as opposed to the dry to mesic fields, prairies, open woods, and forest edges that *D. lanuginosum* inhabits. In all, *D. lindheimeri* and *D. lanuginosum* demonstrate a statistical difference ($P \leq 0.05$) in 15 of the 24 morphological characters sampled. Hitchcock and Chase (1910 and 1951) found these differences striking enough to align *D. lindheimeri* in a separate group (*Spreta*) than *D. lanuginosum*. Gould and Clark (1978) and Freckmann and Lelong (2002, 2003) treated *D. lindheimeri* as infraspecific in their widely encompassing *D. acuminatum*. Though neither of these treatments mentioned the distinctiveness of habitat as evidence for separation, the present study collected habitat information from 70 random herbarium labels of *D. lindheimeri*. Of these, two labels referred to the habitat as "dry," six labels provided no indication of site moisture and 62 labels (89 percent) indicated or implied saturated soil conditions. A similar review of *D. lanuginosum* labels indicated a predominance of dry soils.

Voss (1972) and Voss and Reznicek (2012) noted that along calcareous lake shores in the Great Lakes region, the morphological expression of what is here treated as *Dichanthelium lindheimeri* approximates that of *D. spretum* (a known acidophile). These plants have the overall habit of *D. spretum* coupled with the pubescence characters of *D. lindheimeri*. Furthermore, their vernal inflorescences are open panicles and their spikelets are not pointed, in contrast to *D. spretum* which has narrow inflorescences and pointed spikelets. Additionally, the inflorescences of *D. spretum* are conspicuously more densely flowered. These plants may represent an undescribed taxon within the group that is worthy of further investigation. Perhaps it is because of plants like these that Hitchcock and Chase (1910, 1951) placed *D. lindheimeri* in the informal group "*Spreta*" rather than "*Lanuginosa*." The more typical morphology of *D. lindheimeri* in Michigan seems to be restricted to the southern portion of the lower peninsula (Voss 1972; Voss & Reznicek 2012).

Dichanthelium lindheimeri can occasionally be difficult to differentiate from *D. longiligulatum*. See notes under *D. longiligulatum*, as well as the key above, for distinction between the two.

8. DICHANTHELIUM LONGILIGULATUM (Nash) Freckmann, Phytologia 48: 102.1981. *Panicum longiligulatum* Nash, Bull. Torrey Bot. Club 26: 574. 1899. *Dichanthelium acuminatum* var. *longiligulatum* (Nash) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1127. 1978. *Panicum acuminatum* var. *longiligulatum* (Nash) Lelong, Brittonia 36: 270. 1984. *Dichanthelium acuminatum* subsp. *longiligulatum* (Nash) Freckmann & Lelong, SIDA 20: 168. 2002. **TYPE: USA**. **Florida**. Franklin Co.: Apalachicola, 1892, *Vasey s.n.* (holotype: NY!; isotype: US!).

Plants erect or ascending from a geniculate base, 30–70 cm tall; **internodes** glabrous; **sheaths** glabrous to glabrate; **ligule** 1.8–3.1 mm long (Figure 8a); **pseudoligule** absent; **leaf blades** spreading to ascending, 2–8 cm long, 2.0–6.0 mm wide, adaxial surface glabrous, abaxial surface puberulent; **panicles** 3–8 cm long, half as wide to as wide as long, puberulent and often pilose; **spikelets** 1.1–1.5 mm long, approximately 0.5–0.8 mm wide, elliptic, puberulent to pilose; **first glume** 0.2–0.5 mm long, typically 1/3 as long as the spikelet, obtuse to acute.



Distribution and habitat. In North America *Dichanthelium longiligulatum* is most prevalent along the coastal plain from Mexico to New Jersey. Inland populations are known from several states. Its southern range extends through Central America and northern South America. It is also found throughout the Antilles. The habitat of *D. longiligulatum* consists of seasonally to perennially wet habitats of widely varying degrees of floristic integrity.

Representative specimens. **NICARAGUA**. **Comarca Del Cabo**. 12 Mar 1971, *Seymour 4576* (MO). **USA**. **Florida**. Franklin Co.: 1892, *Vasey s.n.* (NY). **Georgia**. Bulloch Co.: 10 Jun 1901, *Harper 839* (MO). Charlton Co.: 26 Aug 1902, *Harper 1575* (MO). **North Carolina**. Henderson Co.: July 1924, *Davis s.n.* (MO). **Tennessee**. Grundy Co. 23 Jun 1938, *Svenson 9119* (MO).

Dichanthelium longiligulatum can be distinguished from similar members of sect. *Lanuginosa* by its small stature, glabrous sheaths and the general absence of puberulent hairs on the abaxial surfaces of vernal stem leaves. Its overall stature is reminiscent of *D. spretum*, with which it was long aligned in "section" *Spreta* of Hitchcock and Chase (1910, 1951). However, the spikelets of *D. longiligulatum* are smaller than those of *D. spretum* and are not as acute at the apex, the inflorescence is not narrowly paniculate as in typical *D. spretum*, and *D. longiligulatum* has smaller leaf dimensions. *Dichanthelium longiligulatum* also resembles *D. leucothrix*, *D. meridionale*, and *D. wrightianum* but differs from these three in its lack of puberulence on the vernal sheaths, internodes, and adaxial leaf surfaces (mostly). Several authors (Freckmann & Lelong 2002; Freckmann & Lelong 2003; Gould & Clark 1978; Lelong 1984; Zuloaga et al. 1993b) have attempted to place *D. longiligulatum* as a variety or subspecies of *D. acuminatum*. However, *D. longiligulatum* differs strikingly from *D. acuminatum*. *Dichanthelium longiligulatum* has significantly smaller spikelets (1.1–1.5 mm vs. 1.6–2.1 mm), a longer ligule (1.8–3.1 mm vs. 0.4–1.3 mm), lacks the extensive marginal cilia that *D. acuminatum* has on its leaf blades, has glabrous sheaths, and occasionally possesses a light puberulence on the abaxial surfaces of vernal leaves. *Dichanthelium longiligulatum* also has much smaller leaves and is much more densely fascicled in the autumnal form than *D. acuminatum*. The combination of tall, often leaning, stems with dense fascicles of short leaves lends a "string of pearls" appearance. In herbarium specimens from subtropical and tropical regions *D. longiligulatum* often has a grey-green coloration.

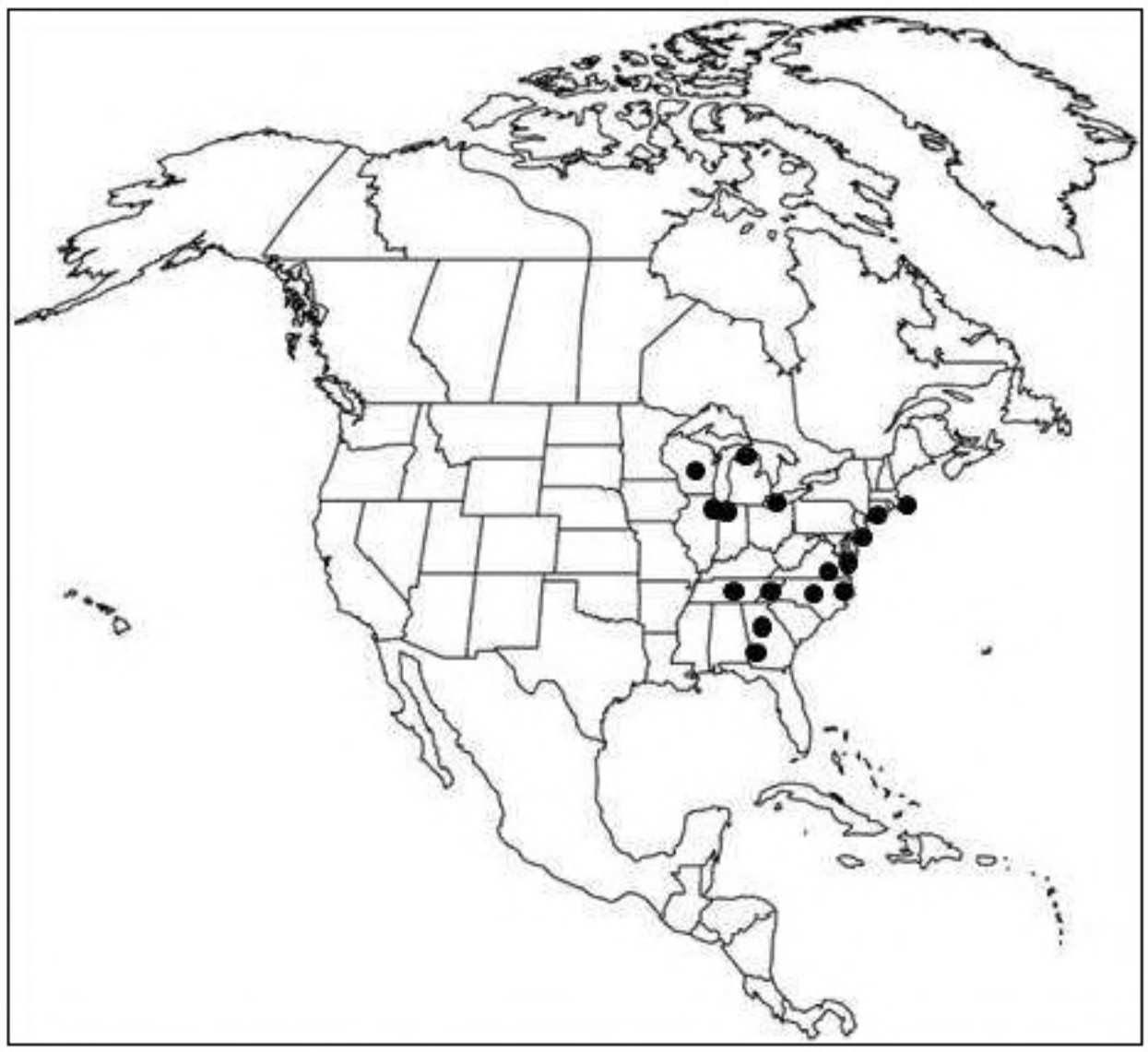
Dichanthelium longiligulatum can occasionally be difficult to differentiate from small leaved forms of *D. lindheimeri*. However, *D. lindheimeri* most often is the size and almost always has the proportions of *D. lanuginosum*. The autumnal form of *D. longiligulatum*, with its dense, nearly spherical, fascicles spaced along what is often a longer wiry stem, is strikingly different from either *D. lindheimeri* or *D. lanuginosum*.

9. DICHANTHELIUM MERIDIONALE (Ashe) Freckmann, Phytologia 39: 270–271. 1978. *Panicum meridionale* Ashe, J. Elisha Mitchell Sci. Soc. 15: 49. 1898. *Panicum unciphyllum* var. *meridionale* (Ashe) Scribn. & Merr., Rhodora 3: 123. 1901. *Panicum lindheimeri* subvar. *meridionale* (Ashe) Farw., Amer. Midl. Naturalist 11: 45. 1928. *Panicum lanuginosum* subvar. *meridionale* (Ashe) Farw., Pap. Michigan Acad. Sci. 26: 5. 1941. **TYPE: USA. North Carolina**. Burke Co.: Blue Ridge, Jun 1893, *Ashe s.n.* (lectotype: US!, designated by Hitchcock and Chase, Contr. U.S. Natl. Herb. 15: 210. 1910).

Panicum albemarlense Ashe, J. Elisha Mitchell Sci. Soc. 16: 84. 1900. *Panicum meridionale* var. *albemarlense* (Ashe) Fernald, Rhodora 36: 76. 1934. *Dichanthelium meridionale* var. *albemarlense* (Ashe) Mohlenbr., Ill. Fl. Illinois (ed. 2): 381. 2001. **TYPE: USA. North Carolina**. Beaufort or Hyde Co.: unknown locality, in open woods, well drained, 26 May 1899, *Ashe s.n.* (lectotype: US!, designated by Hitchcock and Chase, Contr. U.S. Natl. Herb. 15: 220. 1910).

Panicum microphyllum Ashe, J. Elisha Mitchell Sci. Soc. 15: 61. 1898. **TYPE: USA. North Carolina**. Orange Co.: "June," *Ashe s.n.* (NY 381644, designated by LeBlond 2015; duplicate US 2383610-fragm. ex NY 381644).

Plants erect or ascending from a geniculate base, 5–45 cm tall; **internodes** double invested with both short puberulent and long pilose pubescence (Figure 8d); **sheaths** double invested with short puberulent hairs below a pilose or villous pubescence (Figure 8d), longer hairs 1.7–3.8 mm long; **ligule** 1.7–4.0 mm long (Figs. 7a or d); **pseudoligule** absent or intermeshed with ligule; **leaf blades** spreading to ascending, 1.5–7.0 cm long, 2.0–6.0 mm wide, margins ciliate only at the base of blade or eciliate, adaxial leaf surface long pilose, abaxial surface puberulent and occasionally pilose; **panicles** 1.5–5.0 cm long, half as wide to as wide as long, puberulent and pilose; **spikelets** 1.3–1.6 mm long, approximately 0.7–0.9 mm wide, elliptic, puberulent to pilose; **first glume** 0.3–0.8 mm long, typically 1/3 as long as the spikelet, obtuse to acute.



Distribution and habitat. *Dichanthelium meridionale* ranges from Nova Scotia to Minnesota and south to Alabama and Georgia with a predilection for coastal areas. It grows in high quality, seasonally wet or perennially moist sandy soils of open woods, clearings, prairies, and shores.

Representative specimens. **USA**. **Massachusetts**. Barnstable Co.: 3 Jul 1931, *Churchill s.n.* (MO). **New York**. Suffolk Co.: 22 Jun 1916, *Chase 526* (MO). **North Carolina**. Beaufort Co.: *Ashe s.n.* (US). Burke Co.: *Ashe s.n.* (US). Orange Co.: *Ashe s.n.* (NCU). Orange Co.: *Ashe s.n.* (MO). **Tennessee**. Cannon Co.: 20 May 1974, *Kral 52796* (MO). Cannon Co.: 20 May 1974, *Kral 52800* (MO). **Virginia**. Prince George Co.: 30 May 1965, *Freckmann 1565* (MO). Greensville Co.: 18 Jun 1941, *Fernald & Long 12940* (MO).

Gould and Clark (1978) placed *Dichanthelium meridionale* under synonymy with *D. acuminatum* var. *implicatum*. Freckmann and Lelong (2002, 2003) made no mention of where *D. meridionale* fits into their revisions to sect. *Lanuginosa*, but the "Names and Synonyms" section of Volume 25 of the "Flora of North America" lists it as a synonym of *D. acuminatum* subsp. *implicatum*. Neither treatment has provided any direct reason for placing *D. meridionale* into synonymy under *D. acuminatum*. *Dichanthelium meridionale* differs from *D. implicatum* in having a pronounced double vestiture of puberulent hairs beneath a longer pilosity. This is best demonstrated on the sheaths, internodes, and abaxial leaf surfaces of the vernal stem. Because of its extensive double vestiture, *D. meridionale* is often confused with *D. columbianum*. The two can easily be distinguished by the smaller ligule of *D. columbianum* (0.7–1.5 versus 1.7–4.0 mm long). With its small stature, unique combination of pubescence, and affinity to high quality natural areas, *D. meridionale* is one of the more distinctive members of the section.

10. DICHANTHELIUM OVALE (Ell.) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1114. 1978.

Panicum ovale Ell., Sketch Bot. S. Carolina 1: 123. 1816. **TYPE: USA. Georgia**. Camden Co.: St. Mary's, no date, *Baldwin s.n.* (holotype: CHARL; fragment and photo US!).

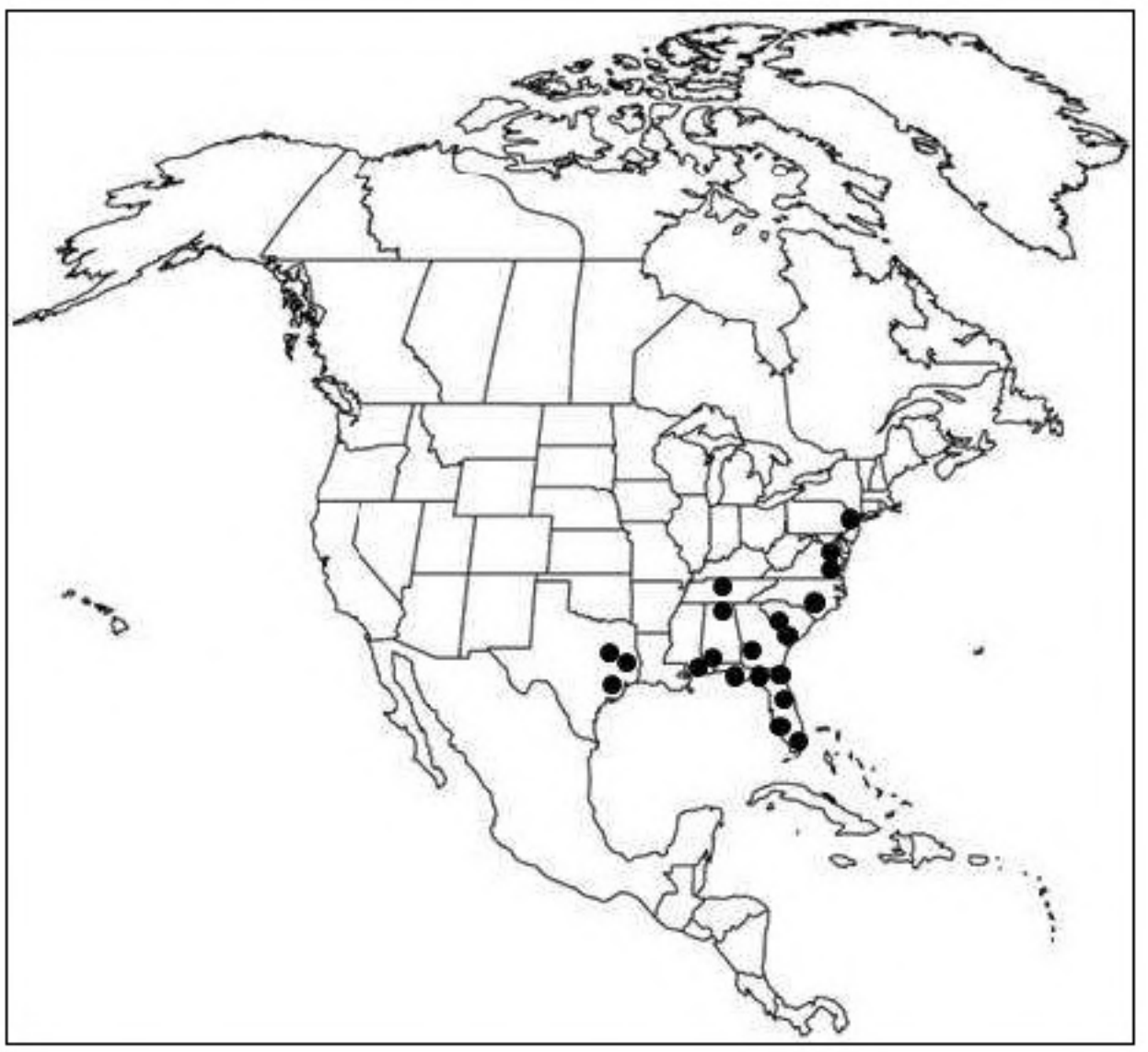
Panicum ciliiferum Nash, Bull Torrey Bot. Club 24: 195–196. 1897. **TYPE: USA. Florida**. Lake Co.: in the vicinity of Eustis, high pine land, 12–31 Mar 1894, *Nash 147* (holotype: NY!; isotypes: US! MO!).

Panicum erythrocarpon Ashe, J. Elisha Mitchell Sci. Soc. 16: 90. 1900. **TYPE: USA. North Carolina**. New Hanover Co.: shady slopes on the sand hills one mile north of Wilmington, 17 May 1899, *Ashe s.n.* (holotype: NCU!; isotypes: NCU, US!).

Panicum wilmingtonense Ashe, J. Elisha Mitchell Sci. Soc. 16: 86. 1900. **TYPE: USA. North Carolina**. New Hanover Co.: shady slopes on the sand hills one mile north of Wilmington, 17 May 1899, *Ashe s.n.* (holotype: NCU!; isotype: US!).

Panicum benneri Fernald, Rhodora 46: 2–3. 1944. **TYPE: USA. New Jersey**. Hunterdon Co.: old field along the Delaware River ca. 1.5 miles east of Raven Rock, 7 Jun 1941, *Benner 9635* (holotype: GH!; isotype: GH!, US, PH).

Plants erect or ascending from a geniculate base, 20–60 cm tall; lower-most **internodes** double invested with short puberulent to pilose hairs below a villous pubescence or occasionally lacking the longer villous hairs, the middle and upper internodes ascending to appressed pilose or villose, lacking the short puberulence of the lower internodes; lowermost **sheaths** double invested with short puberulent hairs below a pilose or villous pubescence (Figure 8d), upper sheaths pilose to villose and lacking puberulent hairs (Figure 8a), longer hairs 0.2–2.7 mm long; **ligule** 0.2–0.7 (–1.0) mm long (Figs. 7b or c); **pseudoligule** 2.0–4.0 mm long when present; **leaf blades** spreading to ascending, 3–11 cm long, 4–10 mm wide, margins ciliate only at the base of blade or eciliate, adaxial leaf surface villose to glabrate, hairs absent along the central third of the blade, abaxial surface with appressed puberulence or glabrate; **panicles** 4–9 cm long, half as wide to as wide as long, puberulent; **spikelets** 2.1–2.9 mm long, approximately 1.0 mm wide, elliptic, pilose; **first glume** 0.7–1.6 mm long, typically 2/5 to 1/2 as long as the spikelet, obtuse **to broadly acute.**



Distribution and habitat. *Dichanthelium ovale* is found along the coastal plain of North America from Massachusetts to Texas and south into Central America. It is likely known from the islands of the Antilles. Its habitat consists of sandy, open woods and clearings.

Representative specimens. **USA**. **Alabama**. Dekalb Co.: 27 May 1974, *Kral 53036* (MO). Henry Co.: Oct 1972, *Kral 48982* (MO). Monroe Co.: 31 May 1972, *Kral 46998* (MO). **Florida**. May 1909, *Chapman s.n.* (MO). Duval Co.: 24 Apr 1897, *Curtiss 5866* (MO). Franklin Co.: 16 May 1969, *Godfrey 69494* (MO). Lake Co.: 17–31 March 1894, *Nash 147* (US). Lake Co.: 13 May 1900, *Curtiss 6616* (MO). Lee Co.: Jul–Aug 1900, *Hitchcock 474* (MO). Liberty Co.: 19 Oct 1977, *Kral 61184* (MO). **Georgia**. *Romer s.n.* (MO). Lee Co.: 11 May 1940, *Duncan 2317* (MO). **Massachusetts**. *Chapman s.n.* (MO). **New Jersey**. Burlington Co.: 16 Jun 1900, *Parker s.n.* (MO). Burlington Co.: 18 Jun 1933, *Herman 4465* (MO). Hunterdon Co.: 7 Jun 1941, *Benner 9635* (GH). Monmouth Co.: 26 Jun 1929, *Churchill s.n.* (MO). **North Carolina**. Cumberland Co.: 16 May 1976, *Solomon s.n.* (MO). New Hanover Co.: 17 May 1899, *Ashe s.n.* (US). Sampson Co.: 17 May 1966, *Freckmann 2114* (MO). **South Carolina**. Aiken Co.: 1 Jun 1867, *Ravenel s.n.* (MO). Aiken Co.: 11 Jun 1867, *Ravenel* (MO). Aiken Co.: 20 May 1899, *Eggert s.n.* (MO). Aiken Co.: 21 May 1899, *Eggert s.n.* (MO). Aiken Co.: Oct 1967, *Ravenel s.n.* (MO). Beaufort Co.: 27 May 1916, *Chase 7115* (MO). Beaufort Co.: 6 May 1917, *Churchill s.n.* (MO). **Tennessee**. Wilson Co.: Jun 1881, *Gattinger 7387* (MO). **Virginia**. Nansemond Co.: 26–28 Jul 1939, *Fernald & Long 10505* (MO). Northumberland Co.: 1 Jun 1946, *Reed 5136* (MO).

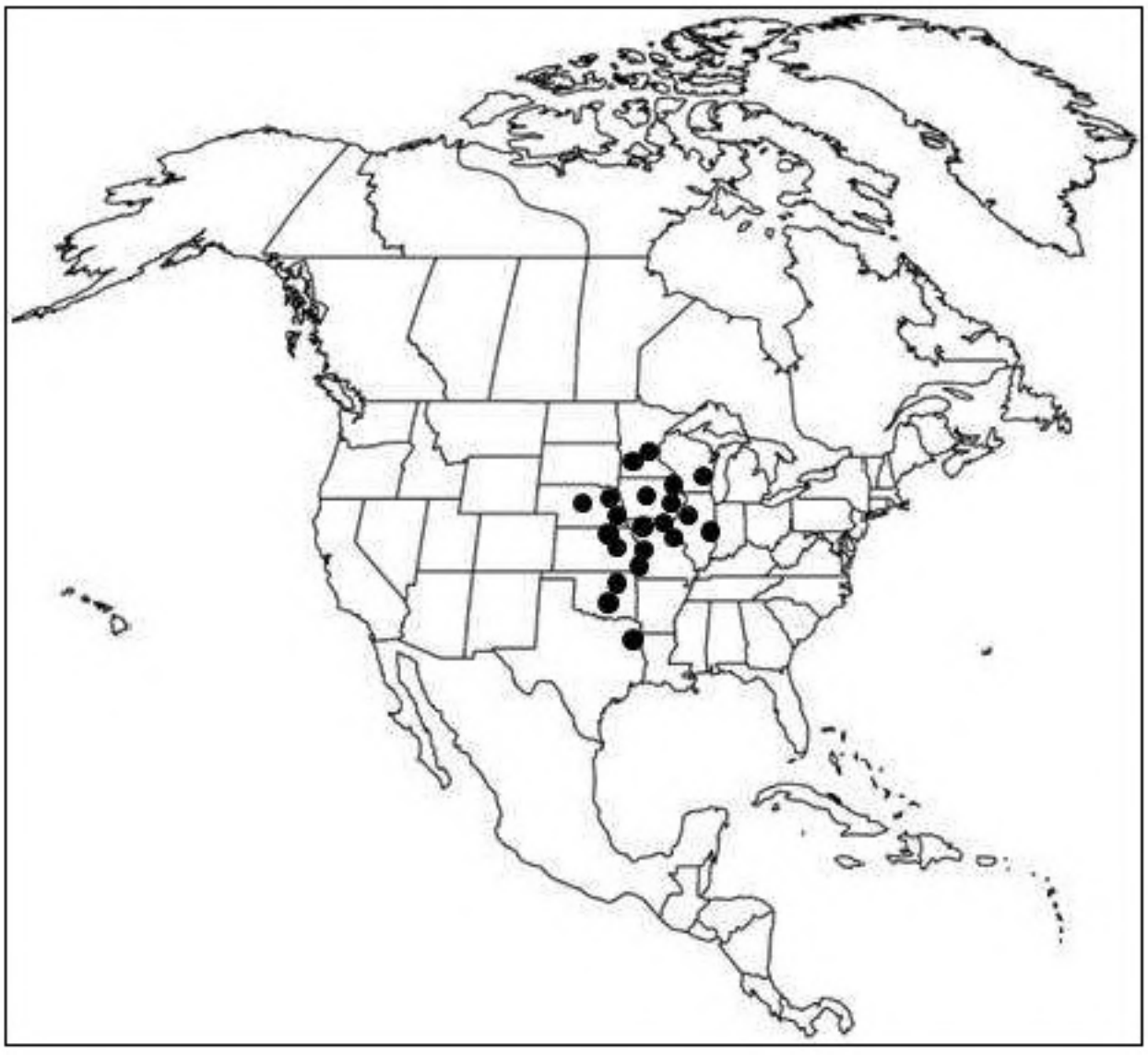
All treatments involving what is now sect. *Lanuginosa* have kept *Dichanthelium ovale* as a distinct species. However, other taxa within the group have often been assigned as infraspecific in *D. ovale*. *Panicum addisonii* (treated under *D. columbianum* in the present work) has often been treated as a variety of *D. ovale*. The treatment of Freckmann and Lelong (2002, 2003) relegated what is here treated as *D. villosissimum* and *D. praecocius* to subspecies of *D. ovale*. Lelong (1984) also treated *D. villosissimum* under *D. ovale* (as *Panicum ovale* var. *villosum*). Interestingly, these are the only two treatments to bridge the gap between the traditional groups *Lanuginosa* and *Columbiana* (now both sect. *Lanuginosa*) of Hitchcock and Chase (1910, 1951) by combining taxa from each group. Lelong (1984) justified this based on Gould and Clark's (1978) placement of *P. addisonii* (including *D. commonsianum*) as a variety of *D. ovale* by stating that *D. villosissimum* is more like *P. addisonii* than *D. ovale* therefore *D. villosissimum* should probably also be a variety of *D. ovale*. However, the present study shows that *P. addisonii* is better placed under *D. columbianum* (for discussion of this see *D. columbianum*) and that *D. villosissimum* and *D. praecocius* demonstrate ample distinction for recognition as separate species.

Dichanthelium ovale differs from both *D. villosissimum* and *D. praecocius* in having larger spikelets, larger first glumes, and a puberulent pubescence on the lower sheaths and internodes of the vernal culms. As with many members of the traditional group *Columbiana*, the hairs on the adaxial surfaces of vernal stem leaves of *D. ovale* are restricted to the blade edges (or lacking altogether), thus the central third of the adaxial leaf surface is glabrous. This is in stark contrast with both *D. villosissimum* and *D. praecocius*, which possess a uniform pubescence across the adaxial leaf surfaces of vernal stem leaves. Furthermore, the true ligule of *D. praecocius* is significantly larger (typically 2.5–4.0 mm) than either *D. villosissimum* (0.3–1.3 mm) or *D. ovale* (0.2–0.7 mm). Freckmann and Lelong (2002) also saw fit to designate *P. pseudopubescens* as a subspecies of *D. ovale*. While this taxon has a convoluted nomenclature, the present study demonstrates that, at least for now, it is best placed in the synonymy with *D. villosissimum*. For additional discussion of *P. pseudopubescens* see notes under *D. villosissimum*. Nomenclatural confusion aside, the only taxon that is likely to be confused with *D. ovale* is *D. commonsianum*. For a discussion on the differences between these two closely related taxa see notes under *D. commonsianum*.

Panicum malacon has often been associated with *D. ovale* (Freckmann & Lelong 2003; Gould & Clark 1978; Hansen & Wunderlin 1988). The present treatment finds that *P. malacon* possesses little morphological resemblance to any members of sect. *Lanuginosa*. Upon review of the type specimen, it is better placed with members of sect. *Angustifolia*.

11. DICHANTHELIUM PRAECOCIUS (Hitchc. & Chase) Mohlenbr., Ill. Fl. Illinois (ed. 2) Grasses: *Panicum* to *Danthonia*: 383. 2001. *Panicum praecocius* Hitchc. & Chase, Rhodora 8: 206–207. 1906. *Panicum lanuginosum* var. *praecocius* (Hitchc. & Chase) Dore, Le Naturaliste Canadien 103: 562. 1976. *Dichanthelium villosissimum* var. *praecocius* (Hitchc. & Chase) Freckmann, Phytologia 39: 270. 1978. *Dichanthelium ovale* subsp. *praecocius* (Hitchc. & Chase) Freckmann & Lelong, Sida 20: 170. 2002. *Panicum ovale* var. *praecocius* (Hitchc. & Chase) Wipff, Sida 20: 1044. 2003. **TYPE: USA. Illinois**. Stark Co.: near Wady Petra, dry bank, 30 Jun 1900, *Chase 649* (holotype: US!; isotypes: NY!, GH!).

Plants erect or ascending from a geniculate base, 10–50 cm tall; **internodes** conspicuously to sparsely pilose to villose (Figure 8a), hairs ascending to appressed; **sheaths** copiously pilose to villose (Figure 8a), the hairs often darkened in hue, erect to ascending and (1.8–) 2.8–4.0 (–4.8) mm long; **ligule** (1.8–) 2.5–4.0 (–4.7) mm long (Figure 8a); **pseudoligule** lacking or indistinguishable from ligule; **leaf blades** ascending, 5–9 cm long, 3–7 mm wide, margins ciliate only at the base of blade or eciliate, adaxial leaf surface villose often with dark hued hairs, abaxial surface pilose; **panicles** 4–6 cm long, half as wide to as wide as long, densely to sparsely pilose, axillary inflorescences produced soon after terminal inflorescences; **spikelets** (1.6–) 1.8–1.9 (–2.1) mm long, approximately 0.8–1.2 mm wide, elliptic, pilose; **first glume** 0.6–1.0 mm long, typically 1/3 to 1/2 the length of the spikelet, acute to broadly acute.



Distribution and habitat. *Dichanthelium praecocius* ranges from southwestern Ontario to North Dakota in the north, east to Illinois, and south to Texas and northwest Arkansas. The habitat of *D. praecocius* primarily consists of upland prairies but rarely extends to open woodlands within or near a prairie matrix. It is endemic to the Tallgrass Prairie Ecoregion. *Dichanthelium praecocius* exhibits high fidelity to intact, undisturbed natural communities and is a good indicator of habitat integrity.

Representative specimens. **USA**. **Arkansas**. Benton Co.: *Plank s.n.* (MO). Benton Co.: 18 Jun 2002, *Thomas 1501* (MO). **Illinois**. Champaign Co.: 20 Jun 1906, *Gleason s.n.* (MO). Stark Co.: 30 Jun 1900, *Chase 649* (US). Stark Co.: 10 Jun 1906, *Chase 671* (MO). **Iowa**. Story Co.: 18 Jun 1865, *Freckmann 1927* (MO). **Kansas**. Cloud Co.: 15 Jun 1937, *Fraser 796* (MO). **Minnesota**. Renville Co.: 19 Jun 1940, *Moore 13054* (MO). Sherburne Co.: 6 Jul 1999, *Swanson 1383* (MO). **Missouri**. Barton Co.: 16 Jun 1990, *Yatskievych & Yatskievych 90-147* (MO). Callaway Co.: 12 Sep 1937, *Steyermark 26220* (MO). Clark Co.: 8 Jul 1909, *Bush 5909A* (MO). Dade Co.: 9 Aug 2000, *Thomas 1307* (MO). Dent Co.: 30 Jun 1929, *Kellogg 15078* (MO). Jasper Co.: 5 Jun 1909, *Palmer 2157B* (MO). Jasper Co.: 5 Jun 1909, *Palmer 2144* (MO). **Nebraska**. Cuming Co.: 31 May 1975, *Churchill 5528* (MO). Lancaster Co.: 15 Jun 1900, *Hedgcock s.n.* (MO). Lancaster Co.: 4 Jun 1973, *Churchill 941* (MO). Saunders Co.: 25 Jun 1974, *Churchill 3588* (MO). Stanton Co.: 15 Jun 1976, *Churchill 7709* (MO). Winneskiek Co.: 12 Jun 1933, *Tolstead s.n.* (MO). **Oklahoma**. Creek Co.: 11 May 1895, *Bush 1220* (MO). Murray Co.: *Waterfall 6021* (MO). **Texas**. Harrison Co.: 8 Aug 1907, *Bush 632* (MO). **Wisconsin**. Columbia Co.: 14 Jun 1942, *Shinners & Shaw 4361* (MO).

Dichanthelium praecocius is unique in the timing of its secondary inflorescence production. Where other *Dichanthelium* produce terminal inflorescences early in the growing season followed by axillary inflorescences late in the season, *D. praecocius* produces both terminal and axillary inflorescences early and continues to produce axillary inflorescences throughout the growing season. In overall morphology it is most similar to *D. lanuginosum* and *D. implicatum*. It differs from both in having larger spikelets, a longer first glume, longer hairs on the vernal sheaths, and a unique distribution of ligule hairs (see key). *Dichanthelium praecocius* also tends to have narrower vernal leaves which are more ascending or appressed than either *D. lanuginosum* or *D. implicatum*. The hairs on the sheaths and adaxial surfaces of *D. praecocius* often have a dark coloration and seem to be more brittle than other species. Because of this, late in the growing season the plants take on a very "messy" appearance with numerous dark, broken and bent hairs. *Dichanthelium praecocius* tends to have smaller vernal inflorescences with fewer nodes on the central axis (average of 7.7) than other members of the section.

When populations of *Dichanthelium lanuginosum* and *D. praecocius* occur sympatrically, as they often do in prairie habitats, they occasionally exhibit what is easily interpreted as introgression wherein the population of *D. lanuginosum* takes on elements of the stature and pubescence characteristics of *D. praecocius*. This may seduce one into the belief that this somehow weakens the species boundaries between the two were it not for the fact that one can readily find *D. lanuginosum* forming the same relationships with *D. oligosanthes* var. *scribnerianum*, *D. linearifolium*, *D. sphaerocarpon*, and *D. scoparium*; four unquestionably distinct species. This is an example of the complex breeding systems and exceptional behaviors that these species exhibit and that necessitate a more flexible and, for lack of a better term, lenient species concept than is usually applied to the genus in general and the section in particular.

Gould and Clark (1978) combined *Dichanthelium praecocius* and *D. villosissimum* and treated the combination as a variety of *D. acuminatum* (*D. acuminatum* var. *villosum*). Freckmann (1978) treated *D. praecocius* as a variety of *D. villosissimum*. Given the present morphological examination, there does not appear to be any infraspecific relationship between any of these three

taxa. Both *D. acuminatum* and *D. villosissimum* have ligules less than 1.4 mm long while that of *D. praecocius* exceeds 1.8 mm long. Although *D. acuminatum* and *D. villosissimum* have similar ligule lengths, the ciliate margins and smaller spikelets of *D. acuminatum* and the dramatically longer vernal sheath pubescence of *D. villosissimum* clearly set each apart. Freckmann and Lelong (2002, 2003) treated both *D. praecocius* and *D. villosissimum* as subspecies of *D. ovale*. For discussion involving these taxa, see notes under *D. ovale*. Populations at the northern and eastern edges of the range of *D. praecocius* are composed of larger, more densely pubescent plants that approximate *D. villosissimum* in terms of gross morphology. Said plants can be distinguished by their longer ligules and smaller spikelets. Plants in the central and western portions of the range have narrower, more appressed leaves and are less densely pubescent overall. These plants more closely resemble *D. implicatum* from which they can be distinguished by having larger spikelets and glumes and longer vernal sheath pubescence (see key for details).

12. DICHANTHELIUM SPRETUM (Schult.) Freckmann, Phytologia 48: 102. 1981. *Panicum spretum* Schult., Mantissa 2: 248. 1824. *Dichanthelium lanuginosum* var. *spretum* (Schult.) Harvill, Castanea 42: 177. 1977. *Dichanthelium acuminatum* subsp. *spretum* (Schult.) Freckmann & Lelong, Sida 20: 168. 2002. **TYPE: USA**. New England, unknown locality, moist ground, no date, *Muhlenberg 184* (holotype: PH; fragment and photo, US!).

Panicum nitidum var. *densiflorum* Rand & Redfield, Fl. Mt. Desert Isl. 174. 1894. *Dichanthelium acuminatum* var. *densiflorum* (Rand & Redfield) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1127. 1978. *Panicum acuminatum* var. *densiflorum* (Rand & Redfield) Lelong, Brittonia 36: 270. 1984. **TYPE: USA. Maine**. Hancock Co.: Mount Desert, shores of Ripples Pond, 28 Jul 1892, *Rand s.n.* (holotype: GH!; fragment, US).

Panicum eatoni Nash, Bull. Torrey Bot. Club 25: 84. 1898. **TYPE: USA. New Hampshire**. Seabrook, unknown locality, 1897, *Eaton s.n.* (holotype: NY!; fragment and photo, US!).

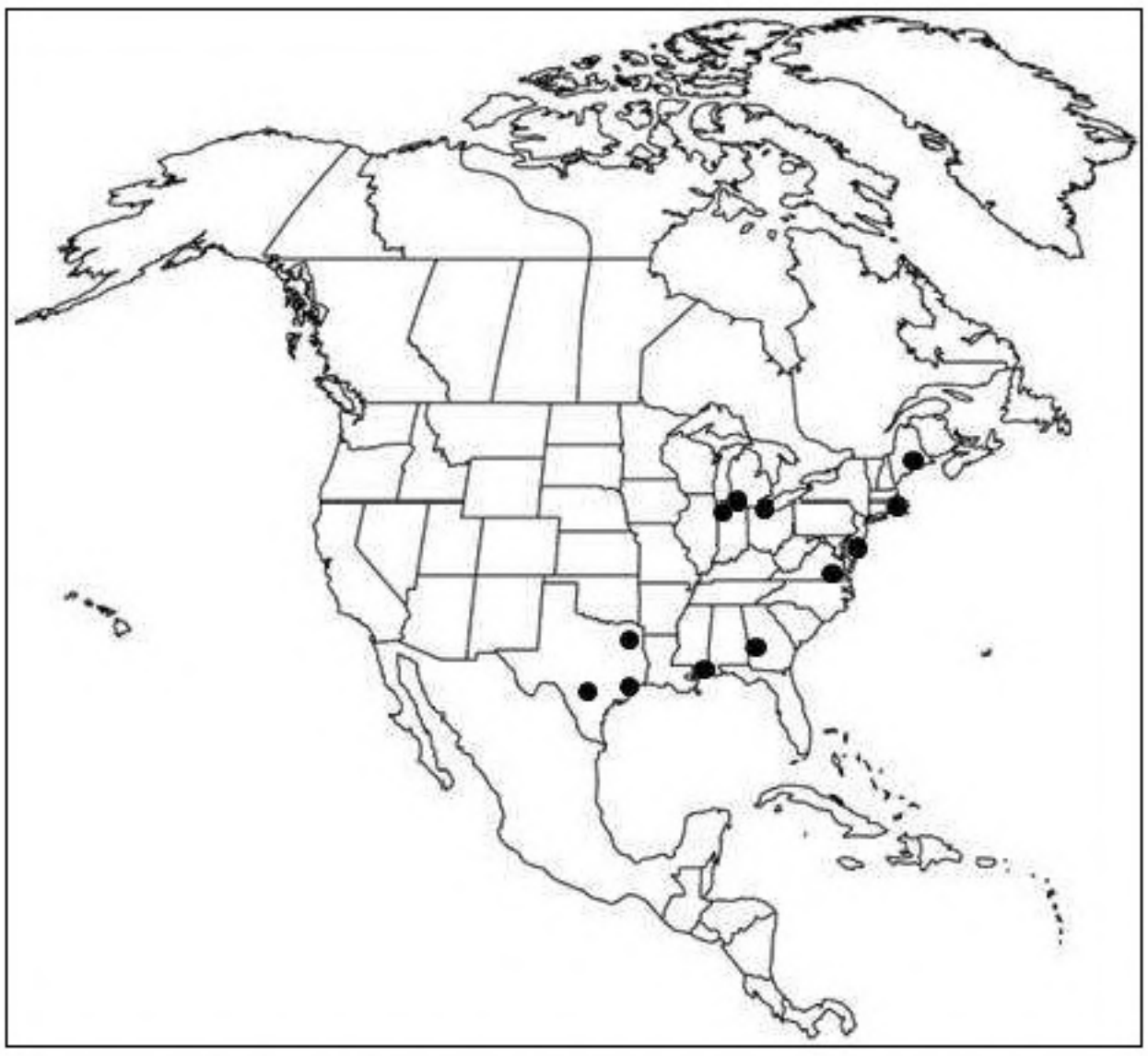
Panicum paucipilum Nash, Bull Torrey Bot. Club 26: 573. 1899. **TYPE: USA. New Jersey**. Cape May Co.: at Wildwood, 30 & 31 May 1897, *Bicknell s.n.* (holotype: NY!; isotypes: NY!, US!).

Panicum octonodum Smith, USDA Div. Agrost. Bull. 17: 73. 1899. *Panicum nitidum* var. *octonodum* Scribn. & Merr., USDA Div. Agrost. Bull. 24: 34. 1901. **TYPE: USA. Texas**. Waller Co.: Waller County line near Harris County, Jun 1898, *Thurow 6* (holotype: US!).

Plants erect or ascending from a geniculate base, 30–120 cm tall; **internodes** glabrous; **sheaths** glabrous; **ligule** 1.7–3.0 mm long (Figure 8a); **pseudoligule** absent; **leaf blades** spreading to ascending, 3–14 cm long, 3.0–9.0 mm wide, glabrous adaxially and abaxially; **panicles** 6–12 cm long, less than half as wide as long, glabrous to sparsely pilose; **spikelets** 1.3–1.9 mm long, approximately 0.7–0.9 mm wide, elliptic to narrowly ovate, pubescent or rarely glabrous; **first glume** 0.3–0.7 mm long, typically 1/4 to 1/3 as long as the spikelet, obtuse to acute.

Distribution and habitat. *Dichanthelium spretum* is found on the coastal plain of North America from Nova Scotia to Texas. It is also found within the Great Lakes Region, where it occurs with other coastal plain disjuncts. It is an acidophile and primarily inhabits saturated to seasonally saturated sandy to peaty soils along lake and bog margins or within coastal marshes and savannas. It is intolerant of natural community disturbance and may be of conservation concern where it is found.

Representative specimens. **USA. Texas**. Waller Co.: Jun 1898, *Thurow 6* (US). **New Jersey**. Cape May Co.: 30–31 1897, *Bicknell s.n.* (NY). **New Hampshire**. Rockingham Co.: 1897, *Eaton s.n.* (NY). **Massachusetts**. Middlesex Co.: 29 Jun 1896, *Blankinship 109* (MO). **CANADA, Nova Scotia**. Yarmouth Co.: 23 Jul 1921, *Fernald, Long & Bartram 23201* (MO). **Indiana**. Porter Co.: 27 Jun 1935, *Tyron Jr. 3718½* (MO). Jasper Co.: 12 Jul 1947, *Friesner 21662* (MO).



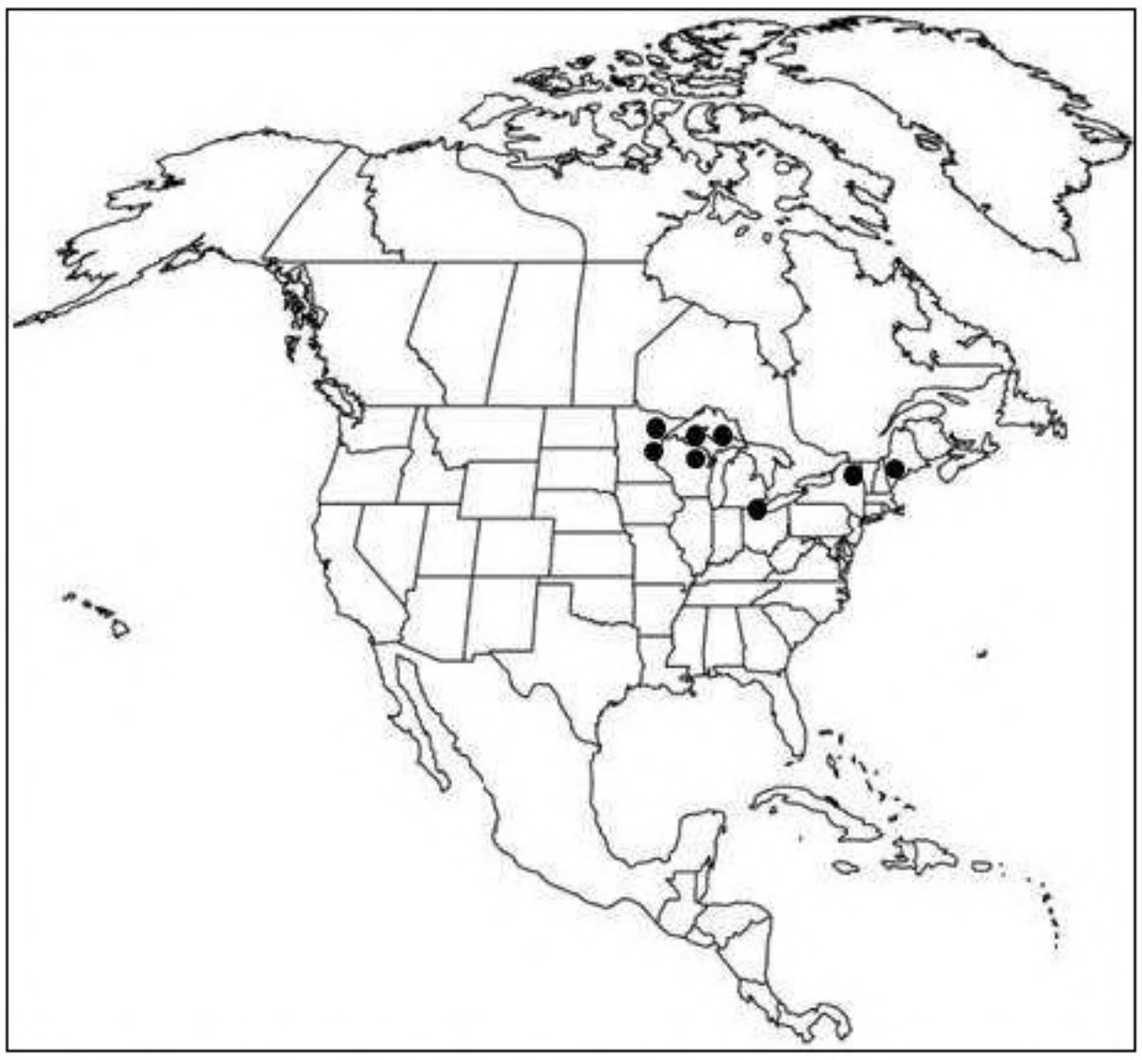
Once the cornerstone of Hitchcock and Chase's (1910, 1951) informal group "*Spreta*", *Dichanthelium spretum* seems a bit out of place within sect. *Lanuginosa*. It differs from all other members of the section in having more acute spikelets, longer sheaths and internodes, and strongly ascending panicle branches (narrow inflorescences). The most morphologically similar species is *D. longiligulatum*, which is smaller in stature, has smaller spikelets, and typically has a wider, more spreading inflorescence. Occasional specimens of *D. spretum* possess glabrous spikelets but this character does not appear to warrant taxonomic recognition. Along calcareous lake shores of the Great Lakes region, *D. lindheimeri* can loosely resemble *D. spretum* (see notes under *D. lindheimeri* for details).

13. DICHANTHELIUM SUBVILLOSUM (Ashe) Mohlenbr., Ill. Fl. Illinois (ed. 2), Grasses: *Panicum* to *Danthonia*, 383. 2001. *Panicum subvillosum* Ashe, J. Elisha Mitchell Sci. Soc. 16: 86. 1900. **TYPE: USA**. **Minnesota**. Carlton Co.: Label from photo of missing holotype (see LeBlond 2015): "Plants of the Southern United States ["Southern" crossed out]. ["Eastern North Carolina" crossed out]," August 1899, *Ashe s.n.* (US 971092, lectotype designated by LeBlond 2015; isolectotypes: NCU 18025, US 971092).

Panicum unciphyllum forma *pilosum* Scribn. & Merr., Rhodora 3: 124. 1901. **TYPE: USA**. **Maine**. Penobscot Co.: 7 Jul 1891, *Fernald 501* (holotype: US!).

Plants erect or ascending from a geniculate base, 10–50 cm tall; lowermost **internodes** pilose to villose and often double invested with short puberulent to pilose hairs (Figure 8b); the middle and upper **internodes** pilose to villose (Figure 8a); lowermost **sheaths** copiously pilose to villose and usually double invested with short puberulent to pilose hairs (Figure 8b), upper sheaths pilose to villose and lacking puberulent hairs (Figure 8a), longer hairs 1.0–2.0 mm long; **ligule** 0.7–1.5 mm long (Figs. 7b or d); **pseudoligule** 1.5–4.0 mm long, distinct or intermeshed with ligule; **leaf blades** spreading to ascending, 2–7 cm long, 3–7 mm wide, margins ciliate only at the base of blade or eciliate, adaxial leaf surface villose to pilose, hairs uniformly distributed, abaxial surface pubescent to pilose; **panicles** 2–6 cm long, half as wide to as wide as long, pilose; **spikelets** 1.6–2.0 mm long,

approximately 1.0 mm wide, elliptic, pilose; **first glume** 0.7–1.0 mm long, typically 1/3 to 1/2 as long as the spikelet, obtuse to broadly acute.



Distribution and habitat. *Dichanthelium subvillosum* is sparsely distributed from Nova Scotia to Saskatchewan in the north, south to New York and Iowa. Its habitat consists of sandy prairies and open woods.

Representative specimens. **USA. Ohio**. Lucas Co.: 17 Jun 1940, *Kriebel 8731* (MO). **Maine**. Oxford Co.: 14 Jun 1931, *Hunnewell 11973* (MO). **Michigan**. Keweenaw Co.: 14 Jul 1956, *Bennett s.n.* (MO). **Minnesota**. Anoka Co.: 30 Jun 1888, *Schuette s.n.* (MO). Carlton Co.: 6 Aug 1899, *Ashe s.n.* (NCU). **New York**. Franklin Co.: 22 Jun 1930, *Muenscher & Maguire 933* (MO). **Wisconsin**. Ashland Co.: 1 Jul 1976, *Coffin 41* (MO). Oneida Co.: 29 Aug 1918, *Coffmann s.n.* (MO).

Though they provided no explanation, Gould and Clark (1978) placed *Dichanthelium subvillosum* in synonymy with *D. acuminatum* var. *acuminatum*. One must assume this placement is based on the superficial similarity of *D. subvillosum* to *P. lanuginosum* var. *fasciculatum* (*D. lanuginosum* in the present treatment), which was also placed in *D. acuminatum*, rather than any direct similarity to actual *D. acuminatum*. Freckmann and Lelong (2002, 2003) took a more conservative approach and elevated var. *fasciculatum* to subsp. *fasciculatum* under *D. acuminatum* and placed *D. subvillosum* as a synonym of this new combination. The present study demonstrates that *D. subvillosum* possesses several morphological characters that warrant specific recognition for this taxon. It differs from *D. lanuginosum* in having a shorter true ligule (0.7–1.5 mm versus 2.0–5.0 mm long), the presence of a distinct pseudoligule, longer first glume (0.7–1.0 mm versus 0.3–0.8 mm long), and less autumnal branching, which is more limited to the base and lower sheaths in *D. subvillosum*. Furthermore, *D. subvillosum* differs strikingly from *D. acuminatum* in that *D. subvillosum* lacks ciliate leaf margins, is more sparsely pubescent, and has longer first glumes in relation to overall spikelet length (first glumes typically 1/3 to 1/2 the spikelet length in *D. subvillosum* versus first glumes typically 1/4 to 1/3 the spikelet length in *D. acuminatum*). The ranges of *D. subvillosum* and *D. acuminatum* are also distinct with *D. subvillosum* occurring in northern North America and *D. acuminatum* occurring in extreme southern North America and southward.

14. DICHANTHELIUM THERMALE (Bol.) Thomas, **comb. nov.** Basionym: *Panicum thermale* Bol., Proc. Calif. Acad. Sci. 2: 181. 1862. *Dichanthelium lanuginosum* var. *thermale* (Bol.) Spellenb., Madrono 23:151. 1975. *Dichanthelium acuminatum* var. *thermale* (Bol.) Freckmann, Phytologia 48: 107. 1981. *Dichanthelium acuminatum* subsp. *thermale* (Bol.) Freckmann & Lelong, Sida 20: 168. 2002. **TYPE: USA. California**. Sonoma Co.: unknown locality, [on hot rocks and in hot water flowing from Geyser springs and Geyser mountains, in the northern part of Sonoma County], no date, *Bolander 3941* (holotype: GH!; isotypes: MO, US).

Plants erect or ascending from a geniculate base, 6.5–42 cm tall; **internodes** of the lower stem double invested with short, often sparse, pilose hairs below a villose pubescence or conspicuously to sparsely pilose (Figs. 7a or b), mid-stem and upper-stem internodes single invested with velutinose to villose pubescence (Figure 8a); **sheaths** conspicuously velutinose to villose, hairs 0.4–3.5 mm long (Figure 8a), the lower stem sheaths singly or double invested with short, pilose hairs (Figure 8b); **ligule** 0.6–3.5 mm long (Figs. 7a, b or d); **pseudoligule** distinct, lacking or intermeshed with ligule, 2–4 mm long; **leaf blades** spreading to ascending, 2–12 cm long, 4–12 mm wide, margins typically ciliate for no more than ¼ the blade length, adaxial leaf surface pilose to densely villose or velutinose, abaxial surface velutinose; **panicles** 4–9 cm long, half as wide to as wide as long, densely to sparely pilose to velutinose; **spikelets** 1.4–2.0 mm long, approximately 0.5–1.0 mm wide, elliptic, pilose; **first glume** 0.4–1.0 mm long, typically equal or less than 1/3 the length of the spikelet, acute to broadly acute.

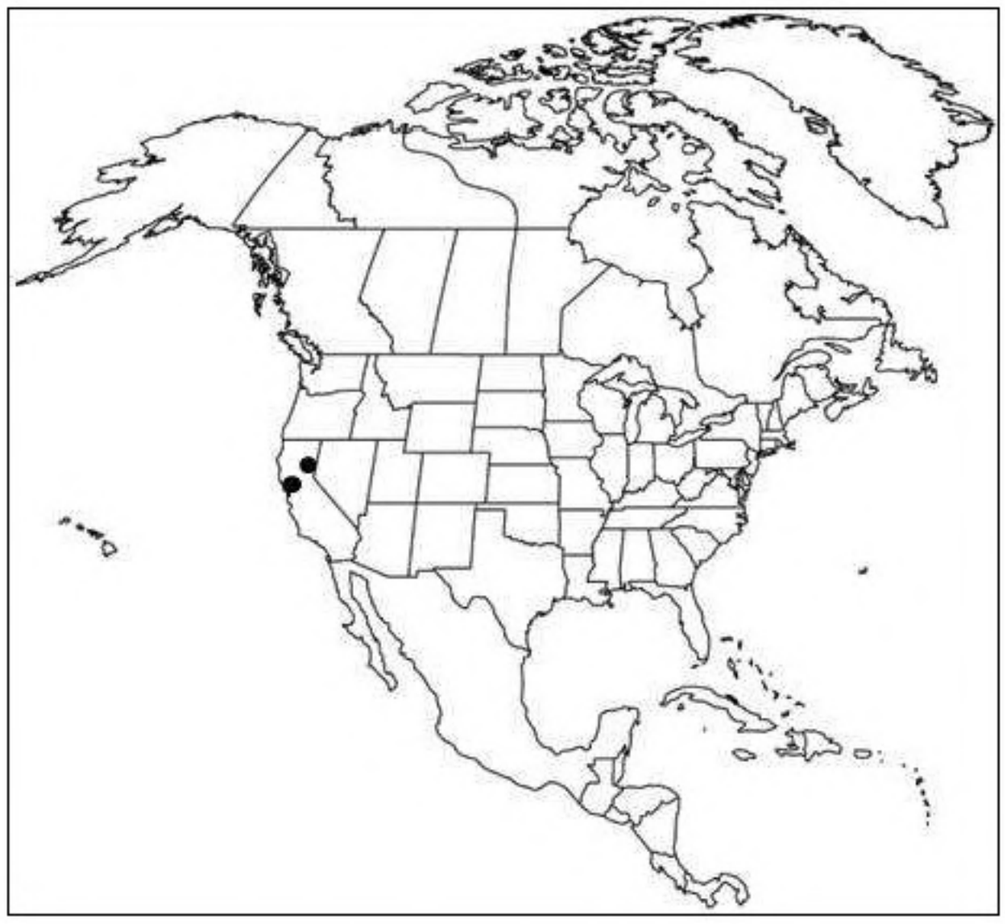
14a. Dichanthelium thermale subsp. **thermale**

Panicum lassenianum Schmoll, Madrono 5: 95–96. 1936. **TYPE: USA. California**. Plumas Co.: Hot Spring Valley, Devil's Kitchen, 6200 ft., 6 Jun 1910, *W.L. Jepson 4082* (holotype: US!; isotype: UC).

Plants erect or ascending from a geniculate base, 12–42 cm tall; **internodes** of the lower stem double invested with short, often sparse, pilose hairs below a villose pubescence (Figure 8b), mid-stem and upper-stem internodes single invested with velutinous to villose pubescence (Figure 8a); **sheaths** conspicuously velutinous to villose, hairs 0.4–2.4 mm long (Figure 8a), the lower stem sheaths double invested with short, pilose hairs (Figure 8b); **ligule** 0.6–1.5 mm long (Figs. 7b or d); **pseudoligule** usually distinct, 2–4 mm long; **leaf blades** spreading to ascending, 2–12 cm long, 4–8 mm wide, margins typically ciliate for no more than ¼ the blade length, adaxial leaf surface densely villose to velutinose, abaxial surface velutinose; **panicles** 4–9 cm long, half as wide to as wide as long, pilose to velutinose; **spikelets** 1.4–2.0 mm long, approximately 0.5–1.0 mm wide, elliptic, pilose; **first glume** 0.5–1.0 mm long, typically equal or less than 1/3 the length of the spikelet, acute to broadly acute.

Distribution and habitat. *Dichanthelium thermale* subsp. *thermale* is only found in the warm, mineral rich soils of isolated hot springs in the Cascade Mountains of northern California.

Representative specimens. **USA. California**: Plumas Co.: 6 Jun 1910, *Jepson 4082* (US). Shasta Co.: Jun 1899, *Greata s.n.* (US). Sonoma Co.: 1865, *Bolander 3991* (MO). Sonoma Co.: 1866, *Bolander 3941* (GH). Sonoma Co.: 27 Aug 1872, *Redfield 9792* (MO). Sonoma Co.: 5 Jul 1931, *Jones 29210* (MO).



Gould and Clark (1978) placed *Dichanthelium thermale* in synonymy with *D. acuminatum*, while Freckmann and Lelong (2003) treated *D. thermale* as a subspecies of *D. acuminatum* (subsp. *thermale*). Given the disjunct range, specialized habitat and morphological autonomy of *D. thermale*, these treatments prove unsatisfying. Morphologically, *D. thermale* differs from *D. acuminatum* in having limited marginal cilia on the vernal leaf blades and by possessing a double vestiture on the culms and sheaths of the vernal stem that *D. acuminatum* lacks. There is significant morphological variation in leaf size, pubescence density, and spikelet length throughout the range of *D. thermale* (Hitchcock & Chase 1910). This could be attributed to inbreeding or genetic drift associated with their isolated populations and the island-like nature of their habitats. Schmoll (1939) attempted to sort out the variation in the *D. thermale* complex. In so doing, she limited *D. thermale* to the hot springs in Sonoma Co., California, described a new species (*P. lassenianum*) for plants occurring in Plumas County (California), described a new species (*P. ferventicola*) from Yellowstone National Park (Wyoming), and described two new varieties of *P. ferventicola* (vars. *papillosum* and *sericeum*), one in the vicinity of Banff, Alberta, and another in Yellowstone National Park. Relative to the differences found in other taxa in the section, the present work could find no meaningful difference between what she called *P. thermale* and *P. lassenianum*, nor was any appreciable difference noted between what she called *P. ferventicola* and *P. ferventicola* var. *papillosum* and var. *sericeum*. Thus, *P. lassenianum* of Schmoll (1939) is here relegated to *D. thermale*. *Panicum ferventicola* and varieties are here treated as *D. thermale* subsp. *sericeum*. However, due to the scarcity of collections and the authors admitted unfamiliarity with the region, the present treatment is not entirely satisfying. The type specimen of *P. ferventicola* seems rather intermediate between the *D. thermale* of California and subsp. *sericeum* of the Rocky Mountains. It is because of this similarity in morphology and habitat that subsp. *sericeum* is linked to *D. thermale* instead of *D. acuminatum* as other authors have contended (Gould & Clark 1978; Freckmann & Lelong 2003). It is tempting to follow the treatment of Hitchcock and Chase (1951), which lumped those taxa described by Schmoll (1939) into *D. thermale* (then as *P. thermale*), but this would be significantly less satisfying given the obvious differences in *D. thermale* and *D. thermale* subsp. *sericeum*. Essentially, the present work serves to provide a basic taxonomic framework that well represents the larger trends in morphological variation for the *D. thermale* complex. In order to more fully elucidate the ultimate taxonomy of these scattered and isolated groups, detailed field studies will be necessary. I suspect the results of such research will more closely resemble the treatment put forth by Schmoll than any work done up to and including the present.

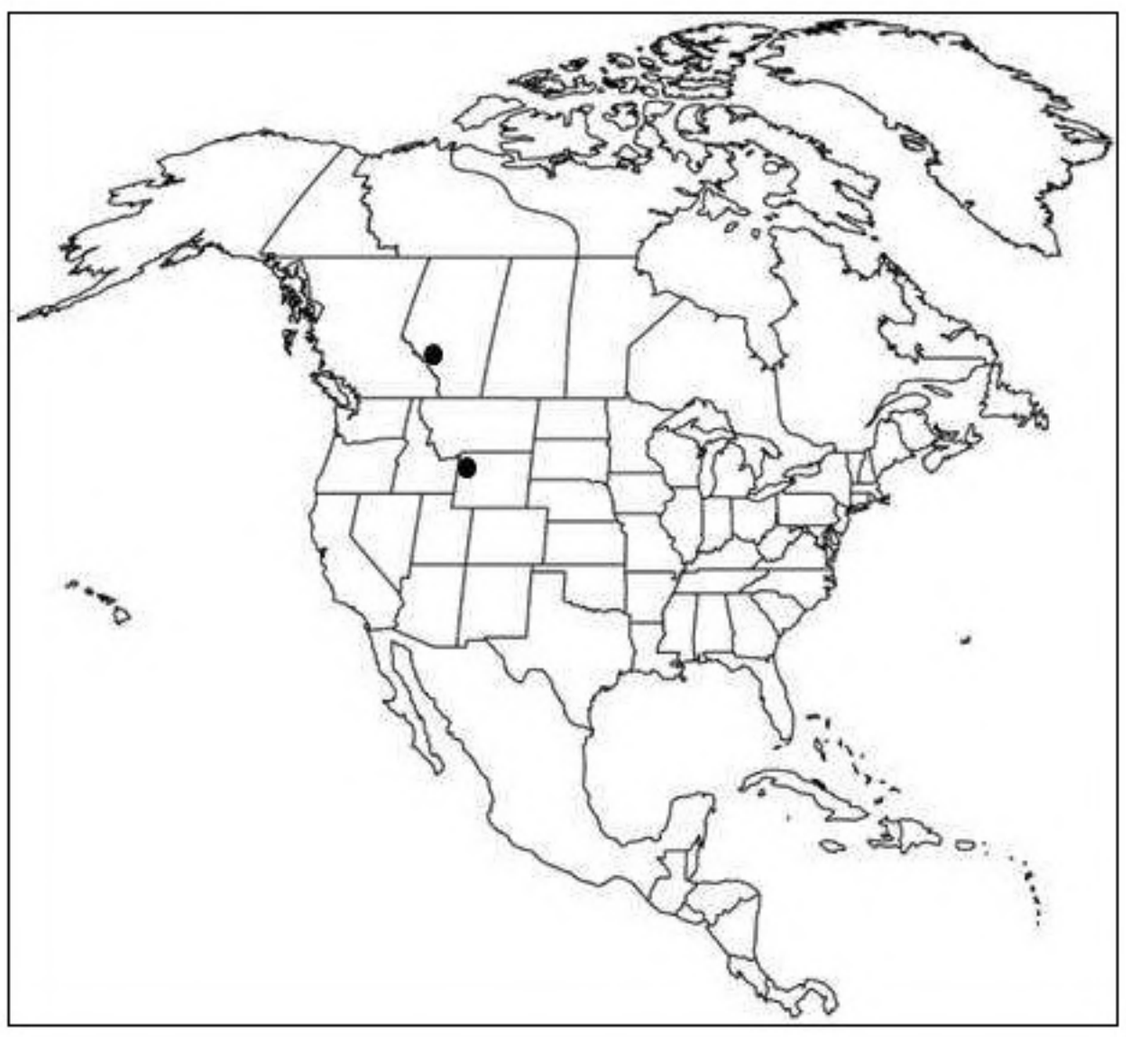
Redman et al. (2002) have demonstrated that *Dichanthelium thermale* possesses a fungal endophyte of the genus *Curvularia*. This endophyte equips *D. thermale* with the heat tolerant proteins and enzymes that allow it to survive soil temperatures in excess of 60°C (Redman et al., 2002). Further research by Marquez et al. (2006) demonstrated even more complexity in the relationship in describing that a virus within the fungus is responsible for the protein stability inferred, secondarily, by the fungal endophyte; resulting in a three-way mutualism. *Dichanthelium thermale* closely resembles *D. subvillosum*, a species of northern North America.

14b. Dichanthelium thermale subsp. **sericeum** (Schmoll) Thomas, **comb. nov.** Basionym: *Panicum ferventicola* var. *sericeum* Schmoll, Madrono 5: 93–94.1939. *Dichanthelium lanuginosum* var. *sericeum* (Schmoll) Spellenb., Madrono 23: 150. 1975. *Dichanthelium acuminatum* subsp. *sericeum* (Schmoll) Freckmann & Lelong, Sida 20: 168. 2002. **TYPE: USA. Wyoming**. Yellowstone National Park, Mammoth Hot Springs, in wet ground about hot springs, 21 Jul 1889, *Nelson & Nelson 6037* (holotype: RM!; isotypes: NY, US!).

Panicum ferventicola Schmoll, Madrono 5: 92–95: 1939. **TYPE: USA. Wyoming**. Park Co.: Yellowstone National Park, 5 mi N of Norris Geyser Basin, 10 Aug 1908, *Chase 5252* (holotype: GH!; isotypes: F!, NY, US!).

Panicum ferventicola var. *papillosum* Schmoll, Madrono 5: 94. 1939. **TYPE: CANADA. Alberta**. Banff, on a declivity wet with water from hot spring, 31 Jul 1914, *Hitchcock 11511* (holotype: GH!; isotypes: F!, NY, US!).

Plants erect to ascending from a geniculate base or forming prostrate mats, 6.5–32 cm tall; **internodes** conspicuously to sparsely pilose (Figure 8a); **sheaths** copiously pilose to velvety villose (Figure 8a), hairs 2.0–3.5 mm long; **ligule** 2.0–3.5 mm long (Figs. 7a or d); **pseudoligule** lacking or intermeshed with ligule; **leaf blades** spreading to ascending, 3–6 cm long, 5–12 mm wide, margins ciliate only at the base of blade or eciliate, adaxial leaf surface pilose to villous with the longest hairs typically 1.5–4.0 mm long, abaxial surface short pilose with the longest hairs typically 0.5–1.5 mm long; **panicles** 3–6 cm long, as wide as long, densely to sparsely pilose; **spikelets** 1.6–1.8 mm long, 0.7–1.0 mm wide, elliptic, pilose; **first glume** 0.4–0.7 mm long, typically 1/4 to 1/5 the length of the spikelet, acute to broadly acute.



Distribution and habitat. *Dichanthelium thermale* subsp. *sericeum* is restricted to the margins of hot springs and geysers in the Rocky Mountains. Verified populations occur in the vicinity of Banff, Alberta, and Yellowstone National Park, Wyoming.

Representative specimens. **CANADA, Alberta**. Banff, 31 Jul 1914, *Hitchcock 220* (GH). **USA. Wyoming**. Teton Co.: 21 Jul 1899, *Nelson & Nelson 6037* (GH). Teton Co.: 10 Aug 1908, *Chase 137* (GH).

A general lack of specimens and a high degree of morphological variation due to isolated populations makes this a difficult taxon to define. However, variations in morphology from the typical subspecies warrant some level of taxonomic recognition (see notes under *D. thermale*). *Dichanthelium thermale* subsp. *sericeum* differs from the typical subspecies in having a long pilose pubescence, a single ligule, and unusually short and wide leaves. Further study involving population level analyses from multiple locations within the range of *D. thermale* will be necessary to fully understand the morphological expression of the *D. thermale* complex.

15. **DICHANTHELIUM VILLOSISSIMUM** (Nash) Freckmann, Phytologia 39: 270. 1978. *Panicum villosissimum* Nash, Bull. Torrey Bot. Club 23:149. 1896. *Dichanthelium lanuginosum* var. *villosissimum* (Nash) Gould, Brittonia 26: 60. 1974. *Dichanthelium ovale* subsp. *villosissimum* (Nash) Freckmann & Lelong, SIDA 20: 170. 2002. **TYPE: USA. Georgia**. Bibb Co.: in the Ocmulgee River swamp, below Macon, 18–24 May 1895, *Small s.n.* (holotype: NY!; isotypes: NY!, US).

Panicum nitidum var. *villosum* A. Gray, N. Amer. Gram. 2: 111. 1835. *Panicum dichotomum* var. *villosum* (A. Gray) Vasey, Dept. Agric. Bot. Div. Bull. 8: 31. 1889. *Dichanthelium acuminatum* var. *villosum* (A. Gray) Gould & Clark, Ann. Missouri Bot. Gard. 65: 1124. 1978. *Panicum acuminatum* var. *villosum* (A. Gray) Beetle, Phytologia 48: 192. 1981. *Panicum ovale* var. *villosum* (A. Gray) Lelong, Brittonia 36: 272. 1984. **TYPE: USA. District of Columbia**. Rock Creek, near Pierce's Mill, 1 Jul 1883, *Vasey s.n.* (lectotype: US!, designated by Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 233. 1910).

Panicum pseudopubescens Nash, Bull. Torrey Bot. Club 26: 577. 1899. *Panicum villosissimum* var.*pseudopubescens* (Nash) Fernald, Rhodora 36: 79. 1934. *Panicum ovale* var. *pseudopubescens* (Nash) Lelong, Brittonia 36: 271. 1984. *Dichanthelium villosissimum* var. *pseudopubescens* (Nash) Mohlenbr., Erigenia 6: 26. 1985. *Dichanthelium ovale* subsp. *pseudopubescens* (Nash) Freckmann & Lelong, Sida 20: 170. 2002. **TYPE: USA. Alabama**. Lee Co.: collected at Auburn, 7 May 1898, *Earle & Baker 1537* (holotype: NY!; isotype: US!).

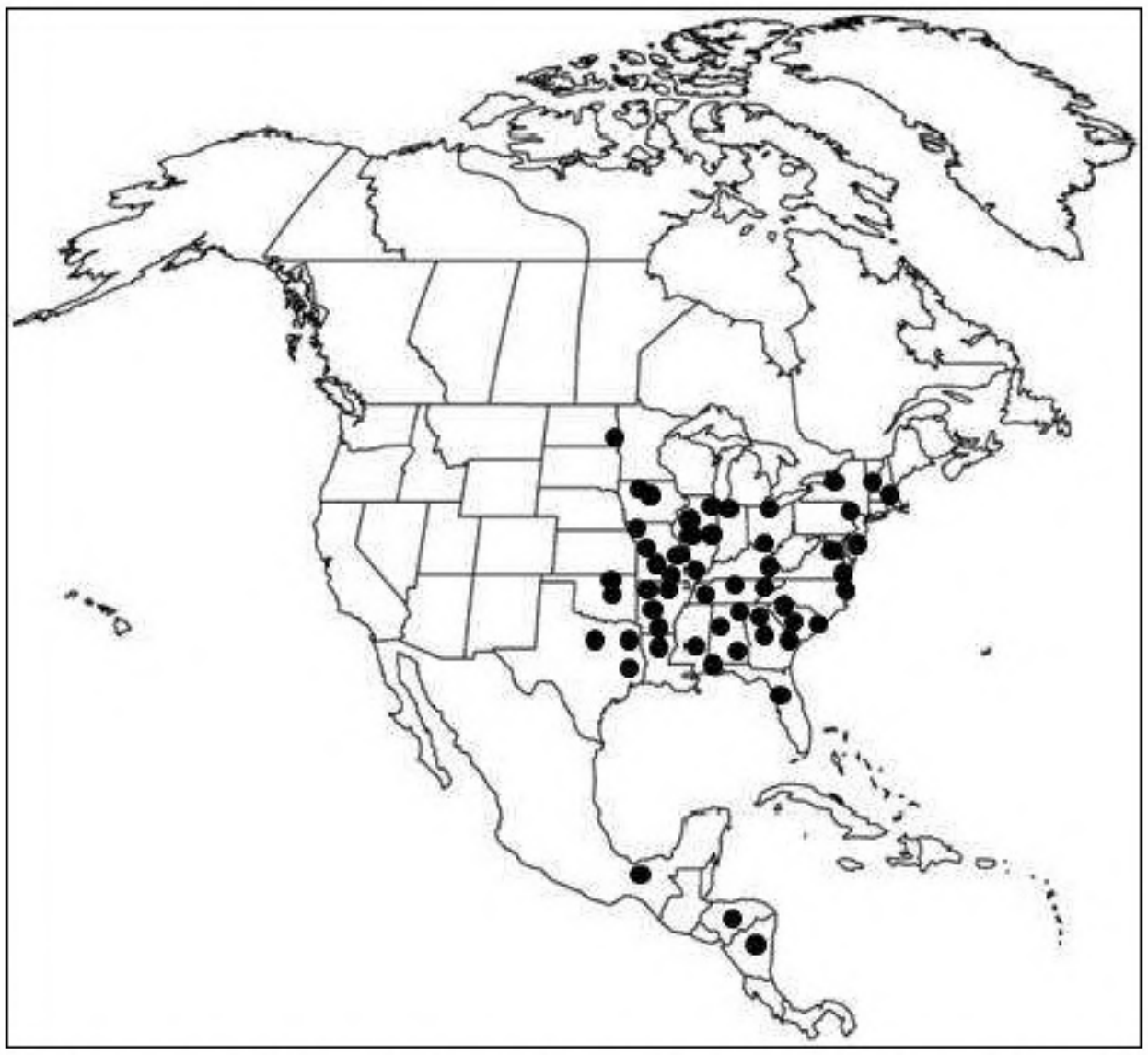
Panicum atlanticum Nash, Bull. Torrey Bot. Club 24: 346–347. 1897. **TYPE: USA. New York**. Kings Co.: on dry somewhat shaded knolls in the grounds of the New York Botanical Garden, 24 Jun 1897, *Nash s.n.* (holotype: NY!; isotype: US!).

Panicum haemacarpon Ashe, J. Elisha Mitchell Sci. Soc. 15: 55. 1898. **TYPE: USA. District of Columbia**. in the vicinity of Washington D.C., 6 Jun 1897, *Kearney s.n.* (lectotype: NY!, designated by Hitchcock and Chase, Contr. U.S. Natl. Herb. 15: 233. 1910; isolectotypes: US!, NCU!).

Panicum xanthospermum Scribn. & Mohr, Contr. U.S. Natl. Herb. 6: 348. 1901. **TYPE: USA. Alabama**. Butler Co.: Greenville, collected in open sandy soil, 8 May 1898, *Mohr s.n.* (holotype: US!; isotype: NY).

Plants erect or ascending from a geniculate base, 10–60 cm tall; **internodes** conspicuously to sparsely villose to long pilose (Figure 8a), hairs ascending to appressed; **sheaths** copiously villose to long pilose, rarely double invested with short pilose pubescence below a long villose pubescence (Figs. 7a or b), erect to ascending and 1.4–3.8 mm long; **ligule** 0.3–1.3 mm long (Figure 8b);

pseudoligule distinct, 2.0–5.0 mm long; **leaf blades** spreading to ascending, 3–11 cm long, 3–12 mm wide, margins ciliate only at the base of blade or eciliate, adaxial leaf surface copiously villose to sparsely pilose with uniformly distributed hairs, abaxial surface pilose; **panicles** 4–10 cm long, half as wide to as wide as long, densely to sparsely pilose to villose; **spikelets** 1.8–2.5 mm long, approximately 0.9–1.2 mm wide, elliptic, pilose; **first glume** (0.6–) 0.8–1.0 (–1.3) mm long, typically 1/4 to 1/3 the length of the spikelet, acute to broadly acute.



Distribution and habitat. *Dichanthelium villosissimum* is found throughout eastern North America from Massachusetts, southern Ontario and Minnesota, south to Texas, Mexico, and into Central America. It is typically found in acidic soils of sand or chert substrate. Throughout its range it is associated with dry pine or oak-hickory forests and woodlands.

Representative specimens. **GUATAMALA**. 13 Sep 1896, *Seler 3235* (MO). **HONDURAS**. **Intibuca**. 21 Jun 1994, *Davidse 35207* (MO). **MEXICO**. **Chiapas**. 5 Nov 1981, *Breedlove 54707* (MO). **USA**. **Alabama**. Butler Co.: 8 May 1898, *Mohr s.n.* (US). Dekalb Co.: 27 May 1974, *Kral 53030b* (MO). Lee Co.: 7 May 1898, *Earl & Baker 1537* (NY). Pickens Co.: 21 May 1960, *McDaniel 1839* (MO). **Arkansas**. Garland Co.: 18 Aug 1937, *Demaree 15843* (MO). **District of Columbia**. 6 Jun 1897, *Kearney Jr. s.n.* (US). 12 Jun 1894, *Holmgren s.n.* (MO). **Georgia**. Bibb Co.: 18–24 May 1895, *Small s.n.* (NY). Dade Co.: 8 May 1948, *Cronquist 5164* (MO). Murray Co.: 18 Jul 1973, *Kral 50687* (MO). Screven Co.: 17 Apr 1948, *Cronquist 5006* (MO). **Illinois**. Cook Co.: 21 Jun 1891, *Moffatt s.n.* (MO). Henderson Co.: *Patterson s.n.* (MO). **Iowa**. *Jones 34* (MO). **Mississippi**. 1858, *Higland s.n.* (MO). **Missouri**. Benton Co.: 24 May 1936, *Steyermark 10744* (MO). Carter Co.: 7 Jun 2001, *Thomas 1399* (private). Ozark Co.: 1 Jul 1937, *Steyermark 22589* (MO). Barry Co.: 6 Jun 1897, *Bush 141* (MO). **New Jersey**. Passaic Co.: 14 Jul 1907, *MacKenzie 2724* (MO). **New York**. Bronx Co.: 24 Jun 1897, *Nash s.n.* (NY). Seneca Co.: 24 Jun 1914, *Randolf 11249* (MO). **North Dakota**. Richland Co.: 27 Jun 1940, *Stevens 459* (MO). **South Carolina**. Bamberg Co.: 17 May 1966, *Freckmann 2133* (MO). Williamsburg Co.: 10 Jul 1939, *Godfrey 428* (MO). **Tennessee**. Hardeman Co.: 14 May 1920, *Palmer 19493* (MO). Knox Co.: Jun 1896, *Ruth s.n.* (MO). Knox Co.: Aug 1894,

Ruth s.n. (MO). **Texas**. Gregg Co.: 18 Jun 1907, *Reverchon s.n.* (MO). Polk Co.: 10 May 1973, *Gould & Hatch 14223* (MO). **Virginia**. Alexandria Co.: 9 Jun 1905, *Chase 555* (MO). Princess Ann Co.: 3 Sep 1905, *MacKenzie 1710* (MO). Norfolk Co.: 11 Jun 1940, *Fernald & Long 11969* (MO).

The most striking features of *Dichanthelium villosissimum* are the density and length of its pubescence. This is especially noticeable on the sheaths and culms of the vernal stem where hairs are often in excess of 3.0 mm long. Past treatments (Ashe 1898; Braun 1967; Deam 1940; Fernald 1950; Gleason & Cronquist 1991; Hitchcock & Chase 1910; Hitchcock & Chase 1951; Jones 1945; Mohlenbrock 1986; Pohl 1947; Radford et al. 1968; Small 1933; Steyermark 1963; Stone 1911; Swink & Wilhelm 1994) involving sect. *Lanuginosa* have maintained *D. villosissimum* as a distinct species, subspecies, or variety. Gould and Clark (1978) treated it as a variety of *D. acuminatum* (*D. acuminatum* var. *villosum*). Beetle (1981) and Zuloaga (1993b) treated it as a variety of *P. acuminatum* (*P. acuminatum* var. *villosum*). However, the present work demonstrates ample morphological resolution to warrant distinction at the rank of species. *Dichanthelium villosissimum* differs from *D. acuminatum* in having significantly larger spikelets, longer sheath pubescence, and a lack of extensive marginal cilia along the blades of the vernal leaves. Freckmann and Lelong (2002, 2003) placed *D. villosissimum* as a subspecies of *D. ovale*. For a discussion of the differences between *D. ovale* and *D. villosissimum* see the notes under *D. ovale* and *D. praecocius*.

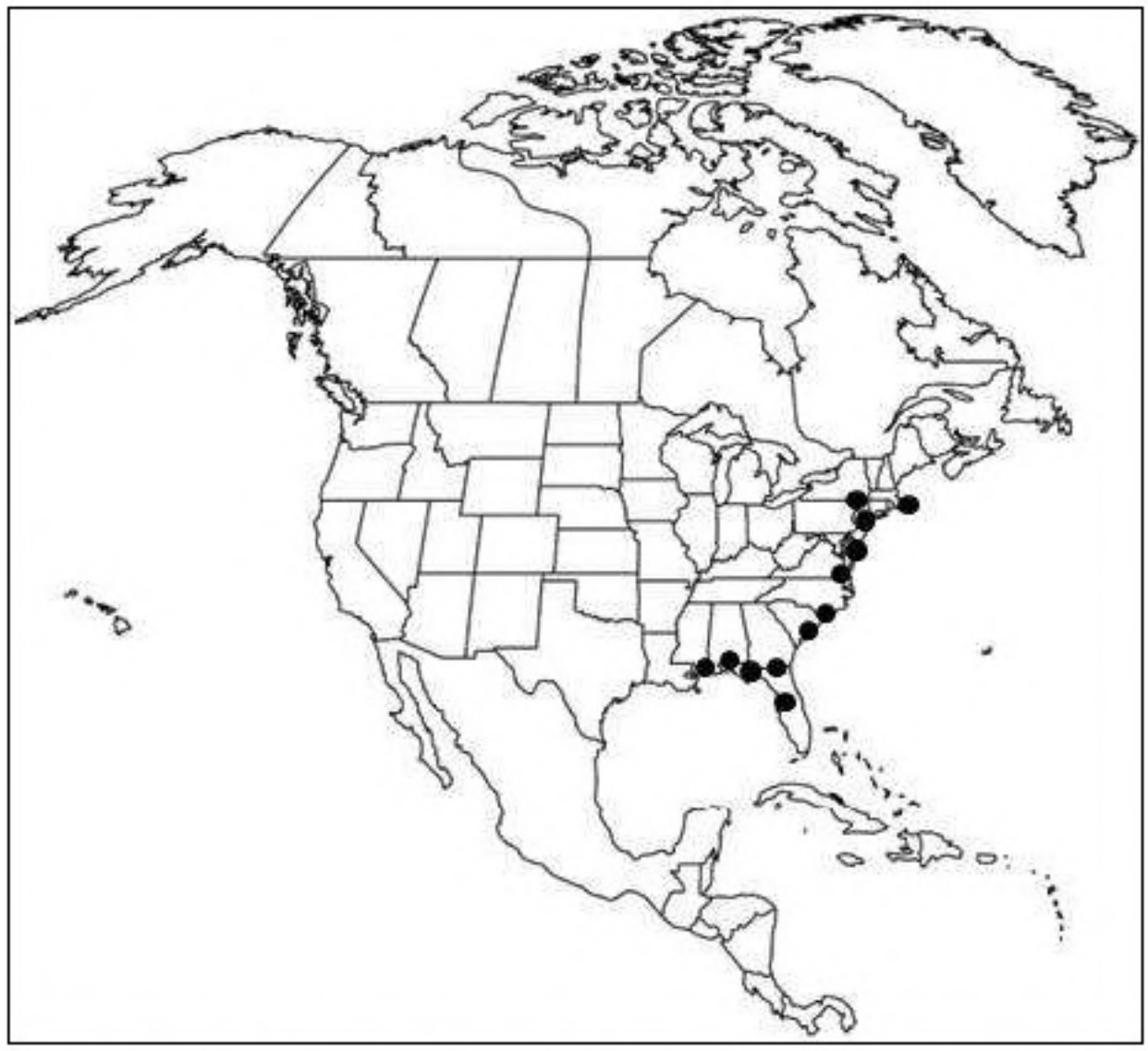
Freckmann and Lelong (2002, 2003) also placed *Panicum pseudopubescens* as a subspecies of *Dichanthelium ovale* and differentiated it from subsp. *villosissimum* (*D. villosissimum* in the present treatment) as having shorter sheath pubescence that is ascending or appressed instead of spreading or retrorse. They further stated that subsp. *pseudopubescens* intergrades morphologically with subsp. *villosissimum*. Though the type specimen of *P. pseudopubescens* does have shorter sheath pubescence than typical *D. villosissimum*, the present study could find no meaningful morphological separation between the two. Nor was any correlation between sheath pubescence length and orientation found. Thus *P. pseudopubescens* is here placed in synonymy with *D. villosissimum*. However, subsequent field experience with this taxon and herbarium investigations, including a re-evaluation of material used in the analysis, suggest that it was likely underrepresented in the database and likely constitutes a definable species. Deam's (1929) and Swink and Wilhelm's (1994) treatments refer to the upper leaf surfaces of *P. pseudopubescens* as being pubescent only along the margins. However, the entity to which they are referring is *P. commonsianum*. This has led to numerous misidentification of Midwestern *D. commonsianum* as *P. pseudopubescens*. The leaf character to which Deam (1929) referred is limited to three taxa within the section (*D. columbianum*, *D. ovale*, and *D. commonsianum*). Morphologically, *D. villosissimum* is closely aligned with and easily confused with *D. praecocius*. For a discussion of the differences see notes under *D. praecocius*.

16. **DICHANTHELIUM WRIGHTIANUM** (Scribn.) Freckmann, Phytologia 48: 101. 1981. *Panicum wrightianum* Scribn., USDA. Div. Agrostol. Bull 11: 44. 1898. *Dichanthelium acuminatum* var. *wrightianum* (Scribn.) Gould & Clark., Ann. Missouri Bot. Gard. 65: 1126. 1978. *Panicum acuminatum* var. *wrightianum* (Scribn.) Reed, Phytologia 80: 284. 1996. **TYPE: CUBA**. unknown locality, 1865, *Wright 3463,* (lectotype: US!, designated by Hitchcock and Chase, Contr. U.S. Natl. Herb. 15: 210. 1910; isolectotypes: GH, MO!, NY, US).

Panicum deminutivum Peck, New York State Mus. Bull. 10: 27. 1907. **TYPE: USA. New York**. Suffolk Co.: Wading River, 20 Aug 1906, *Peck s.n.* (holotype: NY!; isotypes: NY!, US).

Plants erect or ascending from a geniculate base, 5–40 cm tall; **internodes** puberulent and often pilose (Figs. 7c or d); **sheaths** double invested with short puberulent hairs below a pilose or villous pubescence (Figure 8d), the upper merely puberulent (Figure 8c), longer hairs 0.1–0.8 mm long; **ligule** 1.7–3.1 mm long (Figure 8a); **pseudoligule** absent or indistinguishable from ligule; **leaf blades** spreading to ascending, 1.5–4.5 cm long, 2.0–4.5 mm wide, margins ciliate only at the base of

blade or eciliate, adaxial leaf surface puberulent, pilose or both, abaxial surface puberulent; **panicles** 1.5–6.0 cm long, half as wide to as wide as long, puberulent; **spikelets** 0.8–1.0 mm long, approximately 0.4–0.6 mm wide, elliptic, puberulent; **first glume** 0.2–0.4 mm long, typically 1/3 as long as the spikelet, obtuse to acute.



Distribution and habitat. *Dichanthelium wrightianum* ranges along the coastal plain of North America from Massachusetts to Florida and Texas and south through Central America and northern South America. It is also found in the Caribbean Islands. Its habitat consists of saturated to seasonally saturated bogs, savannas, and open woods with sandy, peaty, or mucky soils.

Representative specimens. **CUBA**. 1860-1864, *Wright 3463* (MO). **USA**. **Georgia**. Lowndes Co.: 10 Jul 1968, *Faircloth 5282* (MO). **Florida**. Suwannee Co.: 7 Jun 1900, *Curtiss 6652* (MO). **Massachusetts**. Barnstable Co.: 24 Jun 1909, *Knowlton s.n.* (MO). **Mississippi**. Jackson Co.: 6 May 1898, *Tracy 4885* (MO). **New York**. Delaware Co.: 20 Aug 1906, *Peck s.n.* (US). **North Carolina**. *Bosc s.n.* (US). **Virginia**. Sussex Co.: 6 Jul 1942, *Fernald & Long 14267* (MO).

Given its tiny spikelets and diminutive stature, there is little debate that *Dichanthelium wrightianum* is a distinct species. Morphologically, it is closely aligned with *D. leucothrix*, *D. meridionale*, and *D. longiligulatum*. These four taxa are smaller than others in the section, have relatively small spikelets, and possess varying degrees of puberulence often under a longer pilosity. The extremely small spikelets of *D. wrightianum* easily distinguish it from other members of the section. Gould and Clark (1978) placed *D. wrightianum* as a variety of *D. acuminatum* yet provided no direct evidence for this lumping. Every treatment before and since Gould and Clark (1978) has maintained *D. wrightianum* as a distinct species.

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